SHOUT
SHARE
IT

HARVARD UNIVERSITY

Library of the
Museum of
Comparative Zoology

The Great Basin Naturalist

VOLUME 42, 1982

Editor: Stephen L. Wood

THE GREAT BASIN NATURALIST
BYU PROVO, UTAH
1939

Published at Brigham Young University, by
Brigham Young University

TABLE OF CONTENTS
Volume 42
Number 1 - March 31, 1982

Utah flora: Rosaceae. Stanley L. Welsh 1

Seasonal foods of coyotes in southeastern Idaho: a multivariate analysis. James G. MacCracken and Richard M. Hansen 45

Structure of Alpine plant communities near King's Peak, Uinta Mountains, Utah. George M. Briggs and James A. MacMahon 50

Observations on the reproduction and embryology of the Lahontan tui chub, *Gila bicolor*, in Walker Lake, Nevada. James J. Cooper 60

The prevalence of *Echinococcus granulosus* and other taeniid cestodes in sheep dogs of central Utah. Lauritz A. Jensen, Ferron L. Andersen, and Peter M. Schantz 65

Growth of juvenile American lobsters in semiopen and closed culture systems using formulated diets. S. R. Wadley, R. A. Heckmann, R. C. Infanger, and R. W. Mickelsen 67

Diameter-weight relationships for juniper from wet and dry sites. T. Weaver and R. Lund 73

A description of Timpie Springs, Utah, with a preliminary survey of the aquatic macrobiota. Thomas M. Baugh, Michael A. Nelson, and Floyd Simpson 77

Vegetation and soil factors in relation to slope position on foothill knolls in the Uinta Basin of Utah. Miles O. Moretti and Jack D. Brotherson 81

Weather conditions in early summer and their effects on September blue grouse (*Dendragapus obscurus*) harvest. Joy D. Cedarleaf, S. Dick Worthen, and Jack D. Brotherson 91

Description of the female of *Phalacropsylla hamata* (Siphonaptera: Hystrichopsyllidae). R. B. Eads and G. O. Maupin 96

First record of pygmy rabbits (*Brachylagus idahoensis*) in Wyoming. Thomas M. Campbell III, Tim W. Clark, and Craig R. Groves 100

Paspalum distichum L. var. *indutum* Shinners (Poaceae). Kelly Wayne Allred 101

Local floras of the Southwest, 1920–1980: an annotated bibliography. Janice E. Bowers . 105

The relation between species numbers and island characteristics for habitat islands in a volcanic landscape. Steven H. Carter-Lovejoy 113

Taxonomic studies of dwarf mistletoes (*Arceuthobium* spp.) parasitizing *Pinus strobiformis*. Robert J. Mathiasen 120

Number 2 - June 30, 1982

Utah plant types—historical perspective 1840 to 1981—annotated list, and bibliography. Stanley L. Welsh 129

A new species of *Cryptantha* (Boraginaceae) from Nevada. Kaye H. Thorne and Larry C. Higgins 196

New taxa of thistles (*Cirsium*: Asteraceae) in Utah. Stanley L. Welsh 199

A species of *Cryptantha* (Boraginaceae) dedicated to the memory of F. Creutzfeldt. Stanley L. Welsh 203

Algal populations in Bottle Hollow Reservoir, Duchesne County, Utah. Jeffrey Johansen, Samuel R. Rushforth, and Irena Kaczmarska 205

Herpetological notes from the Nevada Test Site. Wilmer w. Tanner 219

New species of American bark beetles (Coleoptera: Scolytidae). Stephen L. Wood 223

Temperature-related behavior of some migrant birds in the desert. George T. Austin and J. Scott Miller 232
Description of a new *Phalacropsylla* and notes on *P. allos* (Siphonaptera: Hystrichopsyllidae). R. B. Eads and E. G. Campos 241
Vegetation of the mima mounds of Kalsow Prairie. Jack D. Brotherson 246
Occurrence and effect of *Chrysomyxa pirolata* cone rest on *Picea pungens* in Utah. David L. Nelson and Richard G. Krebil 262

Number 3 - September 30, 1982

Buccal floor of reptiles, a summary. Wilmer W. Tanner and David F. Avery 273
Western diamondback rattlesnake in southern Nevada: a correction and comments. Frederick H. Emmerson 350
Prevalence of *Elaeophora schneideri* and *Onchocerca cervipedis* in mule deer from central Utah. Lauritz A. Jensen, Jordan C. Pederson, and Ferron L. Andersen 351
Ecomorphology and habitat utilization of *Echinocereus engelmannii* and *E. triglochidiatus* (Cactaceae) in southeastern California. Richard I. Yeaton 353
First specimen of the spotted bat (*Euderma maculatum*) from Colorado. Robert B. Finley, Jr., and James Creasy 360
Status of introduced fishes in certain spring systems in southern Nevada. Walter R. Courtenay, Jr., and James E. Deacon 361
A new species of *Penstemon* (Scrophulariaceae) from the Uinta Basin of Utah and Colorado. John Larry England 367
Phalacropsis dispar (Coleoptera: Phalacridae), an element in the natural control of native pine stem rust fungi in the western United States. David L. Nelson 369
Species-habitat relationships in an Oregon cold desert lizard community. David F. Werschkul 380
Preliminary index of authors of Utah plant names. L. Matthew Chatterley, Blaine T. Welsh, and Stanley L. Welsh 385
Nest site selection in raptor communities of the eastern Great Basin desert. Dwight G. Smith and Joseph R. Murphy 395
Invertebrate faunas and zoogeographic significance of lava tube caves of Arizona and New Mexico. Stewart B. Peck 405
Additions to the vascular flora of Montana and Wyoming. Robert W. Lichvar and Robert D. Dorn 413

Number 4 - December 31, 1982

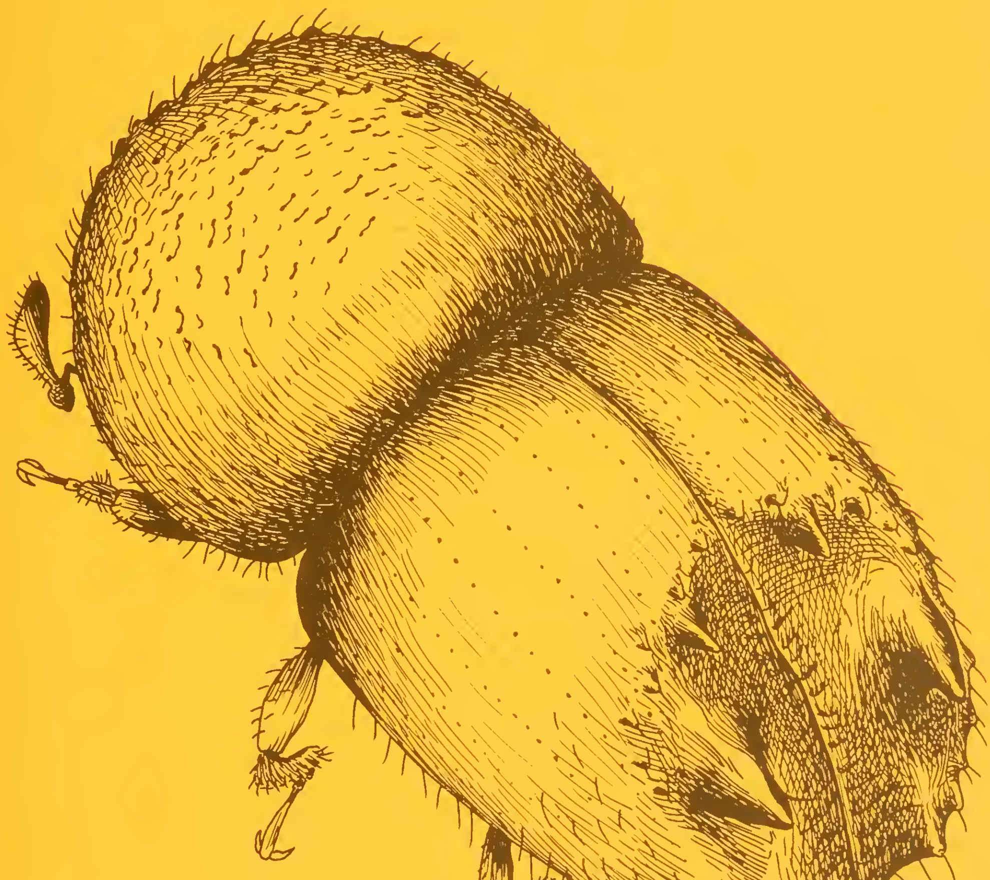
Ants of Utah. Dorald M. Allred 415
Vegetal responses and big game values after thinning regenerating lodgepole pine. D. D. Austin and Philip J. Urness 512
Habitat manipulation for reestablishment of Utah prairie dogs in Capitol Reef National Park. Rodney L. Player and Philip J. Urness 517
Effects of defoliation on reproduction of a toxic range plant, *Zigadenus paniculatus*. V. J. Tepedino 524
Distribution and relative abundance of fish in Ruth Reservoir, California, in relation to environmental variables. Steven Vigg and Thomas J. Hassler 529
Temperature and salinity relationships of the Nevadan relict dace. Steven Vigg 541
Observations on woundfin spawning and growth in an outdoor experimental stream. Paul Greger and James E. Deacon 549

Early development of the razorback sucker, *Xyrauchen texanus* (Abbott). W. L. Minckley and Eric S. Gustafson 553
Behavior and habitat preferences of ring-necked pheasants during late winter in central Utah. Jeffrey G. Skousen and Jack D. Brotherson 562
Rhythm of fecal production and protein content for black-tailed jackrabbits. William D. Steigers, Jr., Jerran T. Flinders, and Susan M. White 567
Prairie dog colony attributes and associated vertebrate species. Tim W. Clark, Thomas M. Campbell III, David G. Socha, and Denise E. Casey 572
Distribution of the moss family Grimmiaceae in Nevada. Matt Lavin 583
Insular biogeography of mammals in the Great Salt Lake. Michael A. Bowers 589
Dorsal hair length and coat color in Abert's squirrel (*Sciurus aberti*). Denis C. Hancock, Jr., and Donald J. Nash 597
The raccoon, *Procyon lotor*, in Wyoming. E. Blake Hart 599
Intercanine crown distances in red foxes and badgers. E. Blake Hart 601

THE GREAT BASIN NATURALIST

Volume 42 No. 1 March 31, 1982 Brigham Young University

MUS. COMP. ZOOL.
LIBRARY
AUG
HARVARD
UNIVERSITY



GREAT BASIN NATURALIST

Editor. Stephen L. Wood, Department of Zoology, 290 Life Science Museum, Brigham Young University, Provo, Utah 84602.

Editorial Board. Kimball T. Harper, Chairman, Botany; James R. Barnes, Zoology; Hal L. Black, Zoology; Stanley L. Welsh, Botany; Clayton M. White, Zoology. All are at Brigham Young University, Provo, Utah 84602.

Ex Officio Editorial Board Members. Bruce N. Smith, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications.

Subject Area Associate Editors.

Dr. Noel H. Holmgren, New York Botanical Garden, Bronx, New York 10458 (Plant Taxonomy).

Dr. James A. MacMahon, Utah State University, Department of Biology, UMC 53, Logan, Utah 84322 (Vertebrate Zoology).

Dr. G. Wayne Minshall, Department of Biology, Idaho State University, Pocatello, Idaho 83201 (Aquatic Biology).

Dr. Ned K. Johnson, Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720 (Ornithology).

Dr. E. Philip Pister, Associate Fishery Biologist, California Department of Fish and Game, 407 West Line Street, Bishop, California 93514 (Fish Biology).

Dr. Wayne N. Mathis, Chairman, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 (Entomology).

Dr. Theodore W. Weaver III, Department of Botany, Montana State University, Bozeman, Montana 59715 (Plant Ecology).

The *Great Basin Naturalist* was founded in 1939 and has been published from one to four times a year since then by Brigham Young University. Previously unpublished manuscripts in English of less than 100 printed pages in length and pertaining to the biological natural history of western North America are accepted. Western North America is considered to be west of the Mississippi River from Alaska to Panama. The *Great Basin Naturalist Memoirs* was established in 1976 for scholarly works in biological natural history longer than can be accommodated in the parent publication. The *Memoirs* appears irregularly and bears no geographical restriction in subject matter. Manuscripts are subject to the approval of the editor.

Subscriptions. The annual subscription to the *Great Basin Naturalist* for private individuals is $16.00; for institutions, $24.00 (outside the United States, $18.00 and $26.00); and for student subscriptions, $10.00. The price of single issues is $6.00 each. All back issues are in print and are available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to Brigham Young University, *Great Basin Naturalist*, 290 Life Science Museum, Provo, Utah 84602. The *Great Basin Naturalist Memoirs* may be purchased from the same office at the rate indicated on the inside of the back cover of either journal.

Scholarly Exchanges. Libraries or other organizations interested in obtaining either journal through a continuing exchange of scholarly publications should contact the Brigham Young University Exchange Librarian, Harold B. Lee Library, Provo, Utah 84602.

Manuscripts. See *Notice to Contributors* on the inside back cover.

6-82 650 59839

ISSN 017-3614

The Great Basin Naturalist

Published at Provo, Utah, by
Brigham Young University

ISSN 0017-3614

Volume 42 March 31, 1982 No. 1

UTAH FLORA: ROSACEAE

Stanley L. Welsh[1]

Abstract.— A revision of the rose family, Rosaceae, is presented for the state of Utah. Included are 115 species and 9 varieties of indigenous and introduced plants in 35 genera. A key to the genera and species is provided, along with detailed descriptions, distributional data, and pertinent comments. Proposed as a new taxon is *Crataegus douglasii* Lindl. var. *duchesnensis* Welsh. New combinations include *Potentilla concinna* Richards var. *bicrenata* (Rydb.) Welsh & Johnston; *P. concinna* var. *modesta* (Rydb.) Welsh & Johnston; *P. concinna* var. *proxima* (Rydb.) Welsh & Johnston; *P. glandulosa* Lindl. var. *micropetala* (Rydb.) Welsh & Johnston; *P. ovina* J. M. Macoun var. *decurrens* (Wats.) Welsh & Johnston; *P. pensylvanica* L. var. *paucijuga* (Rydb.) Welsh & Johnston.

This paper is one of a series of taxonomic revisions leading to a definitive treatment of the flora of Utah. The rose family is of moderate size in the state, but it is important for the indigenous species that comprise portions of the plant communities of substance. The family is important, too, for its introduced ornamental and fruit plants. Apples, pears, raspberries and relatives, cherries, peaches, plums, apricots and relatives, and strawberries are important products of orchards and gardens.

Introduced taxa number 44, or 38 percent of the total rosaceous flora reported herein. Half of those taxa belong to genera not represented in the indigenous flora. Practically all of the introduced taxa are cultivated ornamental or fruit plants. It is a remarkable family to have so few weedy species. Only *Geum* and *Potentilla* support species which are weedy, but some of the cultivated fruit plants or their rootstocks that escape can become problems. The Himalayan blackberry escapes and persists as a spiny bramble in lower elevation agricultural regions.

The most difficult and largest genus in the family in Utah is *Potentilla*. That genus presents an amazing array of intergrading taxa, which have been subjected to a series of interpretations. The extreme interpretations involve recognition of an infinite number of taxa at species rank on the one hand, and the subjugation of most of these in synonymy of broadly defined species on the other. The treatment of *Potentilla* presented here is the result of collaboration between me and Barry C. Johnston of the U.S. Forest Service, in Denver. It strikes a position somewhere between the extremes, and represents a compromise between the views of the authors. We have chosen to avoid the use of the segregate generic names, except to indicate their position in the key to the species, and to present the synonymy that will allow use by those who might be so inclined.

---

[1] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

ROSACEAE

Rose Family

Annual, biennial, or perennial herbs, shrubs, or trees; leaves alternate or basal (and still alternate) or less commonly opposite, simple or pinnately to palmately compound, mostly deciduous, stipulate or rarely exstipulate; flowers perfect or imperfect, regular, complete or incomplete, perigynous to epigynous, borne singly or in racemose, corymbose, umbellate or cymose clusters; sepals usually 5 (more in some), often bearing bracteoles alternate with the lobes, borne with petals and stamens on margin of a hypanthium; petals usually 5 (lacking or more in some), commonly showy; stamens 5 to numerous; pistils 1 to many, of 1 carpel, or of 5 connate or distinct carpels enclosed in the hypanthium; fruit an achene, follicle, drupe, pome, aggregate, hip, or accessory. The rose family is both large and complex. The diversity of fruit type reflects the many morphological differences in structure of the gynoecium in this assemblage. Suggestions by some workers that the group should be segregated into more than one family is not without merit. They are held together by the presence of the hypanthium on which the perianth and stamens are displayed. This is a complex structure, with several possible origins, and might fail ultimately as a diagnostic character.

1. Plants annual, biennial, or perennial herbs .... Subkey I.
— Plants trees, shrubs, or subshrubs .... Subkey II.

Subkey I.

1. Petals lacking; flowers numerous, borne in dense spikes; leaves pinnately compound .... *Sanguisorba*
— Petals present; flowers not both numerous and borne in spikes 2
2(1). Leaves bi- or triternately dissected into linear segments; petals white; plants of Piute, Beaver, and Sevier counties .... *Chamaerhodos*
— Leaves various, but not bi- or triternately dissected into linear segments; petals white, yellow, or pink 3
3(2). Flowers solitary on scapose peduncles; leaves simple, crenate; fruit of plumose achenes; sepals and petals 8–10 each .... *Dryas*
— Flowers usually more than 1; leaves compound or lobed, rarely simple; fruit not of plumose achenes; sepals and petals usually 5 each 4
4(3). Bractlets lacking between the sepals; flowers with a stalked receptacle; hypanthium funnelform; plants of Washington Co. .... *Purpusia*
— Bractlets present, alternating with the sepals; flowers with a sessile receptacle; hypanthium not funnelform 5
5(4). Leaflets tridentate apically, entire along the sides; stamens 5; plants prostrate or mat forming, of high elevations .... *Sibbaldia*
— Leaflets variously toothed or lobed, but not regularly tridentate apically; stamens 5, 10, or more; plants of various habit and habitat 6
6(5). Leaves trifoliate; plants with well-developed stolons; flowers white; receptacle ripening into an accessory fruit .... *Fragaria*
— Leaves mostly with more than 3 leaflets, but, if trifoliolate, then lacking stolons; flowers mostly yellow; receptacle not ripening 7
7(6). Leaflets very numerous, mostly less than 6 mm long; petals usually clawed .... *Ivesia*
— Leaflets 3–15 (rarely more), commonly much more than 6 mm long; petals sessile 8

8(7). Leaves palmately or pinnately lobed or compound, not lyrate pinnatifid; styles at maturity not elongate and conspicuous .... *Potentilla*
— Leaves pinnately lobed or compound or more usually lyrate-pinnatifid; styles at maturity elongate and conspicuous .... *Geum*

Subkey II.

1. Leaves compound 2
— Leaves simple 7

2(1). Stems and/or leaves armed with prickles or spines 3
— Stems and leaves lacking prickles or spines 4

3(2). Pistils several, enclosed within a fleshy hypanthium; fruit a hip; petals very showy .... *Rosa*
— Pistils several to many, on an elongate receptacle; fruit an aggregate; petals not especially showy .... *Rubus*

4(2). Leaves bipinnately compound, the ultimate segments 0.5–1.5 mm long; herbage glandular-stellate, aromatic .... *Chamaebatiaria*
— Leaves once pinnately compound, the leaflets much longer than 1.5 mm; herbage not glandular-stellate 5

5(4). Leaflets 3–7; leaves 1.5–3.5 cm long; flowers yellow; low shrub .... *Potentilla*
— Leaflets 7–15 or more; leaves 5–20 cm long or more; flowers white to cream; moderate shrubs to small trees 6

6(5). Ovary superior; stamens 20 or more; leaflets 13–23; cultivated shrubs .... *Sorbaria*
— Ovary inferior; stamens 15–20; leaflets 9–15; indigenous shrubs or cultivated trees .... *Sorbus*

7(1). Leaves opposite; petals lacking; intricately branched, low desert shrubs of southern and southeastern Utah .... *Coleogyne*
— Leaves alternate; petals present (lacking in *Cercocarpus*); plants of various habits and habitats 8

8(7). Shrubs low, mat forming; flowers solitary or in dense spikes on leafless or merely bracteate scapes 9
— Shrubs or small trees, never mat forming; flowers various, but neither scapose nor subscapose 10

9(8). Flowers solitary, the sepals and petals mostly 8–10 each; leaves crenate; plants of alpine tundra .... *Dryas*
— Flowers in dense spikes, the sepals and petals commonly 5 each; leaves entire; plants of rock surfaces at low to moderate elevations .... *Petrophytum*

10(8). Pistils superior, the 1 to several separate or partially connate; ovaries not adnate to the hypanthium; fruit a drupe, aggregate, achene, follicle, or capsule 11
— Pistils inferior, the 3- to 5-carpellate ovaries adnate to the hypanthium; fruit a pome 21

11(10). Flowers inconspicuous; petals lacking; leaves entire and evergreen (except in *C. montanus*) .... *Cercocarpus*
— Flowers showy, though small in some; petals present; leaves mainly toothed or lobed, often deciduous 12

12(11). Pistil 1; fruit a drupe; leaves commonly with glands at base of blade or on petiole .... *Prunus*

— Pistils 1 to many; fruit not a drupe; leaves not gland-bearing 13

13(12). Leaves pinnately veined, the lobes, if any, pinnate 14

— Leaves palmately veined, the lobes palmately arranged or flabellate 16

14(13). Flowers yellow, solitary, terminating branches of the current year .... *Kerria*

— Flowers white to pink or lavender, borne in corymbs, panicles or racemes 15

15(14). Flowers borne in racemes, 1.5 cm wide or more; petals 6–12 mm long .... *Exochorda*

— Flowers borne in corymbs or panicles, less than 1 cm wide; petals 6–15 mm long .... *Spiraea*

16(13). Flowers large, 2 cm broad or more, in few-flowered cymes; fruit an aggregate . ... *Rubus*

— Flowers commonly less than 2 cm broad, solitary or in corymbs or panicles 17

17(16). Flowers numerous, borne in panicles .... *Holodiscus*

— Flowers borne singly or in few- to many-flowered corymbs 18

18(17). Flowers borne in umbellate corymbs; leaves broad and thin, commonly 1–6 cm wide or more .... *Physocarpus*

— Flowers borne singly or in corymbose racemes; leaves thickish, seldom to 1 cm wide 19

19(18). Pistils numerous; petals white; leaf lobes tightly revolute; plants of low elevations in southern Utah .... *Fallugia*

— Pistils 1–5 (rarely more); petals white to cream or pale yellowish; leaf lobes not tightly revolute; plants of broad distribution 20

20(19). Pistils 1 or 2; styles not plumose; leaves usually 3-lobed .... *Purshia*

— Pistils commonly 5 (or more); styles plumose at maturity; leaves commonly 5- to 7-lobed .... *Cowania*

21(10). Stems armed with thorns or spines 22

— Stems unarmed 24

22(21). Leaves evergreen, crenate-serrate; pomes commonly orange; petals white, less than 4 mm long .... *Pyracantha*

— Leaves deciduous, serrate or doubly serrate; pomes variously colored, rarely orange; petals more than 5 mm long 23

23(22). Shrubs to 2 m tall (generally less); flowers 20–45 mm broad; fruit over 2 cm thick .... *Chaenomeles*

— Shrubs or small trees to 5 m tall or more; flowers 9–18 mm broad; fruit less than 1.5 cm thick .... *Crataegus*

24(21). Leaves entire or essentially so 25

— Leaves serrate to doubly serrate (see also *Peraphyllum*) 27

25(24). Leaves ovate to cordate ovate, 1.5–5 cm wide or more; pomes clothed with a villous tomentum .... *Cydonia*

— Leaves variously shaped, less than 1.5 cm wide; pomes glabrous 26

26(25). Shrubs to 1.5 m tall or more, indigenous; leaves narrowly elliptic; fruit an acrid pome .... *Peraphyllum*

— Shrubs of various height, cultivated; leaves ovate to obovate or oblanceolate; pomes mealy, nonacrid .... *Cotoneaster*

27(24). Flowers white, in racemes; plants indigenous, rarely cultivated; leaves prominently toothed toward the apex .... *Amelanchier*

— Flowers white or otherwise, in corymbs; plants cultivated, sometimes escaping; leaves toothed or lobed throughout 28

28(27). Leaves deeply or at least prominently lobed .... *Sorbus*

— Leaves moderately, if at all, lobed 29

29(28). Shrubs to 2 m tall (generally less); flower solitary or sessile in corymbose clusters .... *Chaenomeles*

— Shrubs or trees to 7 m tall or more; flowers pedicellate in corymbose or umbellate clusters 30

30(29). Flowers in umbels; styles connate at the base; fruit with few if any stone cells, apple-shaped .... *Malus*

— Flowers in corymbs; styles free; fruit with stone cells, mostly pear shaped .... *Pyrus*

AMELANCHIER Medic.

Shrubs or small trees with unarmed branches; leaves alternate, simple, not lobed; stipules linear, caducous; flowers perfect, regular, borne in racemes; hypanthium short, with a glandular disk on the inner surface; sepals 5, persistent; petals 5, white; stamens usually 10 or more; pistil 1, the ovary inferior, usually 5-loculed (appearing as 10); styles 2–5, the stigmas capitate; fruit a reddish to purplish, often glaucous, pome.

JONES, G. N. 1946. American species of *Amelanchier*. Ill. Biol. Monogr. 20: 1–126.

1. Leaves mainly over 2.5 cm long; petals mostly 9–15 mm long; style commonly 5 .... *A. alnifolia*

— Leaves mainly less than 2.5 cm long; petals 5–10 mm long; styles 2–4 (rarely 5) .... *A. utahensis*

***Amelanchier alnifolia* (Nutt.) Nutt.** Serviceberry, Shadbush, Saskatoon. [*Aronia alnifolia* Nutt.; *Pyrus alnifolia* (Nutt.) Lindl.; *A. canadensis* var. *alnifolia* (Nutt.) T. & G.; *A. canadensis* var. *pumila* Nutt. in T. & G.; *A. pumila* (Nutt.) Roem.; *A. alnifolia* var. *cusickii* (Fern.) C. L. Hitchc.; *A. polycarpa* Greene]. Low shrubs to small trees, mostly 2–5 m tall; leaves petiolate, mainly 20–50 mm long, 15–40 mm broad, oval to oblong, acute to rounded or subcordate basally, rounded to truncate apically, serrate near the apex, glabrous or hairy on one or both sides; flowers in short racemes; sepals 2.8–4.6 mm long; petals 9–15 mm long, 3.3–5.8 mm wide, spatulate-oblanceolate, white to pinkish; styles 5 (or 4); fruit purplish to black purple, glaucous, subglobose, 6–14 mm long, palatable. Streamsides, meadows, and mountain slopes at 1500 to 2900 m in sagebrush, mountain brush, aspen and mixed conifer woods in Box Elder, Cache, Davis, Garfield, Iron, Millard, Morgan, Piute, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Weber, and Washington counties; Alaska and Yukon east to Hudson Bay and south to California, Arizona, New Mexico, and Nebraska. Attempts to segregate the various proposed infraspecific taxa among our Utah materials are fraught with difficulties not easily overcome, even by application of mechanical and arbitrary keys. Pubescence or its absence and the position of that pubescence form the basis of the main segregates. The feature of pubescence seems to be so variable, not only within *A. alnifolia*, but within *A. utahensis* (q.v.), that it might indicate a response to ecological conditions rather than genetic affinities. More work is indicated; 66 (iii).

***Amelanchier utahensis* Koehne** Utah Serviceberry. [*A. bakeri* Greene; *A. oreophila* A. Nels.; *A. utahensis* ssp. *oreophila* (A. Nels.) Clokey; *A. florida* var. *oreophila* (A. Nels.) R. J. Davis; *A. crenata* Greene; *A. elliptica* A. Nels.; *A. prunophila* Greene; *A. rubescens* Greene; *A. utahensis* var. *cinerea* Goodding, type from Washington Co.]. Low to large shrubs, mostly 0.5–4 m tall, intricately branched, often in dense clumps; leaves petiolate, mainly 10–27 mm long, 6–27 mm wide, oval to ovate, oblong, or elliptic, acute to rounded or subcordate basally, rounded to truncate or less commonly acute apically, serrate near the apex, hairy on one or both sides, rarely glabrous; sepals 1–3 mm long; petals 5.2–10 mm long, 1.8–4.2 mm wide, spatulate-oblanceolate to elliptic, white, cream or pinkish; styles 2–4 (5); fruit purplish or pinkish, 5–12 mm long, palatable or dry and hardly edible. Streamsides, dry slopes, or thickets in sagebrush, grassland, mountain mahogany, mountain brush, pinyon-juniper, aspen, and ponderosa pine communities at 900 to 2800 m in all counties in Utah (type from Leeds, Washington Co.); Washington to Montana and south to Baja California, Arizona, New Mexico, and Texas. Segregation of all specimens in the *alnifolia-utahensis* complex is difficult if not impossible. Diagnostic features show overlap, and, although trends are apparent in the vast amount of material available, the best of characteristics fail singly and often in combination as well. Because of the trends indicated by leaf and petal size and other features, it seems best to treat *A. utahensis* apart from the tangled morphology of *A. alnifolia*. Additionally, variation within the *utahensis* assemblage is as great as (or greater) than that known to occur in the *alnifolia* materials; 193 (xxvi).

CERCOCARPUS H. B. K.

Shrubs or small trees with unarmed branches and very dense wood; leaves alternate, simple, entire or toothed; stipules small, adnate to petiole; flowers perfect, regular, borne solitary or in small clusters, terminal or axillary; hypanthium trumpetlike, with a deciduous apical portion; sepals 5; petals lacking; stamens 10 or more, borne in 2 or 3 [Bsw; pistils 1, of 1 carpel; style terminal; fruit an achene, with the elongate plumose style persisting.

MARTIN, F. L. 1950. A revision of *Cercocarpus*. Brittonia 7: 91–111.

1. Leaves deciduous, toothed, not especially revolute .... *C. montanus*
— Leaves evergreen, entire or toothed, decidedly revolute 2
2(1). Leaves (at least some) toothed; a hybrid .... *C. montanus* X *C. ledifolius*
— Leaves entire 3
3(2). Leaves elliptic, commonly 12–30 mm long or more; shrubs or small trees, mostly of middle and higher elevations .... *C. ledifolius*
— Leaves linear to narrowly oblong, usually less than 12 mm long; low intricately branched shrubs of lower middle and lower elevations .... *C. intricatus*

Cercocarpus intricatus **Wats.** Dwarf Mountain Mahogany. [*C. ledifolius* var. *intricatus* (Wats.) Jones; *C. intricatus* var. *villosus* Schneid., type from Deep Creek, Juab (?) Co.; *C. arizonicus* Jones]. Shrubs mostly 0.5–2 m tall, intricately branched; leaves 3–18 mm long, 0.8–1.4 mm wide, oblong to linear (rarely elliptic), tightly revolute, glabrous, strigose-pilose, or villous, coriaceous and persistent; flowers 3.2–8.7 mm long; sepals 0.6–1.2 mm long; stamens 10–20; tails of achenes 1–3 cm long. Rimrock, cliffs, and slopes in desert shrub, pinyon-juniper and mountain brush communities at 1370 to 2400 m in Beaver, Emery, Garfield, Grand, Juab, Kane, Millard, San Juan, Sanpete, Sevier, Uintah, Utah (type from American Fork Canyon), Washington, and Wayne counties; Nevada, California, and Arizona. Pubescence of leaves varies in form from strigose-pilose to crinkly-hairy, or is lacking. Plants with pilose leaves form the basis of var. *pilosa*, but the feature does not seem to be correlated with any other. Leaves are heavily cutinized in plants from Kane and Washington counties; 53(xiii).

Cercocarpus ledifolius **Nutt. in T. & G.** Curl-leaf Mountain Mahogany. [*C. ledifolius* var. *intercedens* Schneid.; *C. ledifolius* var. *intercedens* f. *subglaber* Schneid., type from Slate Canyon, Utah Co.; and f. *hirsutus* Schneid., type from Ogden, Utah]. Shrubs or small trees, mainly 2–5 m tall; leaves 10–42 mm long, 2–14 mm wide, elliptic to oblong, the margin only revolute, pubescent to glabrous, coriaceous, persistent; flowers 7–10 mm long; sepals 1.2–2.1 mm long; stamens 20–30; tails of achenes 4.5–8 cm long. Mountain brush, pinyon-juniper, aspen, and spruce-fir communities, often in stands, at 1400 to 3000 m in Beaver, Box Elder, Cache, Carbon, Emery, Garfield, Grand, Iron, Juab, Millard, Morgan, Piute, Rich, Sanpete, Summit, Tooele, Uintah, Utah, Washington, Wasatch, and Weber counties; Washington to Montana and southward to California, Arizona, and Colorado. Hybrids are known between *C. ledifolius* and *C. montanus*. They are easily discerned by the coriaceous persistent toothed leaves. They occur as scattered individuals in places of contact between the parental types. Similarly, putative hybrids involving *C. ledifolius* and *C. intricatus* are known. Longer, very narrow, and markedly revolute leaves mark those apparent hybrids; 89(xi).

Cercocarpus montanus **Raf.** Alder-leaf Mountain Mahogany. [*C. betuloides* Nutt. in T. & G.; *C. betulaefolius* Nutt. ex Hook.; *C. parviflorus* var. *glaber* Wats.; *C. parviflorus* var. *betuloides* (Nutt.) Sarg.; *C. montanus* var. *glaber* (Wats.) Martin; *C. parvifolius* var. *minimus* Schneid.; *C. flabellifolius* Rydb., type from Glenwood, Sevier Co., Utah]. Shrubs, or less commonly, small trees commonly 1.2–4 m tall; leaves short-petiolate, the blade obovate to oblanceolate or orbicular, 6–44 mm long, 5–23 mm wide, crenate-serrate, glabrous above, pubescent beneath (sometimes glabrous), deciduous; flowers 9.5–17.5 mm long; sepals 0.9–1.7 mm long; stamens 25–40, the anthers hairy; tails of achenes 3–10 cm long. Mountain brush, sagebrush, grassland, pinyon-juniper, aspen, and mixed conifer communities at 1400 to 2800 m throughout Utah; Oregon to Wyoming and south to Mexico. This and other species of *Cercocarpus* are valuable browse plants for wildlife and domestic livestock. They are components of wild seed mixtures in reclamation attempts; 91(xiv).

CHAENOMELES Lindl.

Shrubs, usually armed with thorns; leaves alternate, simple, serrate, stipules large, deciduous; flowers perfect, regular, solitary or 2–5 or more in sessile clusters; hypanthium short; sepals not persistent; petals 5 (sometimes more), variously colored; stamens 20 or more; pistil 1, the ovary inferior, usually 5-loculed; styles 5, joined at the base; the stigmas capitate; fruit a pome of moderate size.

1. Branchlets with verrucose small scars left by deciduous short hairs; flowers orange scarlet, about 2.5 cm wide; plants mostly less than 1 m tall .... *C. japonica*
— Branchlets smooth, lacking hair scars; flowers variously colored, over 2.5 cm wide; plants commonly more than 1 m tall .... *C. speciosa*

Chaenomeles japonica **(Thunb.) Lindl. ex Spach.** Japanese Quince. [*Pyrus japonica* Thunb.; *Cydonia japonica* (Thunb.) Pers; *Cydonia lagenaria* Lois.; *Cydonia japonica* var. *lagenaria* (Lois.) Makino; *Chaenomeles lagenaria* (Lois. Koidz.]. Shrubs to 1 m tall (rarely more); the short branchlets often modified as thorns, the young branchlets with deciduous short hairs leaving verrucose scars on falling; leaves obovate, 20–50 mm long, 8–35 cm wide, obtusely serrate, obtuse to subacute apically; flowers orange scarlet, about 2.5 cm wide; fruit subglobose, about 3 cm thick. Cultivated ornamental in Carbon, Salt Lake, and Utah counties; introduced from Japan; 4(i).

Chaenomeles speciosa **(Sweet) Nakai** Flowering Quince. [*Cydonia speciosa* Sweet; *C. lagenaria* Koidz. not (Lois.) Koidz.]. Shrubs to 2 m tall, the short branchlets often modified as spines, glabrous or with short deciduous hairs leaving no scars on falling; leaves oblong to ovate or lanceolate, 22–65 mm long, 12–35 mm wide, sharply serrate, acute to subacute apically; flowers scarlet to white or red, 2.5–3.5 cm wide; fruit subglobose to pyriform, 2–5 cm thick. Cultivated ornamental in Juab, Salt Lake, and Utah counties; introduced from China; 3(i).

CHAMAEBATIARIA (Porter) Maxim.

Aromatic shrubs, unarmed; leaves alternate, bi- or tripinnately compound, the herbage stellate-pubescent; stipules herbaceous, more or less persistent; flowers perfect, regular, showy, borne in terminal panicles; hypanthium turbinate; sepals 5, persistent; petals 5, white; stamens many; pistils 5, more or less connate below, the ovary superior; styles 5; fruit of follicles.

Chamaebatiaria millefolium **(Torr.) Maxim.** Fern Bush, Desert Sweet. [*Spiraea millefolium* Torr.]. Shrub 8–20 dm tall (rarely more), the stems and herbage glandular and stellate-pubescent when young; leaves 0.9–6.7 cm long, 0.4–1.8 cm wide, oblong to lanceolate in outline, with 8–24 pairs of pinnae, these again pinnate, the tertiary segments again pinnatifid; panicles 3–15 cm long; flowers 0.8–1.5 cm wide; sepals ovate to lanceolate, 3–5 mm long, green; petals white, 2.5–5 mm long and about as broad; follicles 4–6 mm long, few seeded. Sagebrush, mountain brush, aspen, limber pine, and spruce-fir communities at 1800 to 2900 m in Beaver, Box Elder, Garfield, Iron, Juab, Kane, Millard, Piute, Tooele, and Washington counties; Oregon, Idaho, Wyoming, and south to California and Arizona; 34 (vii).

CHAMAERHODOS Bunge

Plants biennial or short-lived perennial herbs; leaves alternate and in a basal rosette, bi- or triternately divided, the segments narrow; stipules foliose, narrowly oblong, simple or divided, persistent; flowers perfect, regular, borne in bracteate, corymbose cymes; hypanthium cup shaped, long-hairy within; sepals 5; petals 5; stamens 5, borne at the base of the petals; pistils 5 (rarely fewer), distinct, the ovaries superior, each 1-loculed; styles 1 per pistil, the stigma capitate; fruit an achene.

Chamaerhodos erecta **Bunge in Ledeb.** American Chamaerhodos. [*C. erecta* var. *nuttallii* T. & G.; *C. erecta* ssp. *nuttallii* (T. & G.) Hulten; *C. nuttallii* (T. & G.) Rydb.]. Plants erect, mostly 7–28 (30) cm tall, from a taproot and a basal rosette, the stems freely branched above the base; leaves mostly 7–40 mm long, the ultimate segments linear to oblong, sparingly long-hairy; cymes equaling ¼ to ½ the plant height; flowers short-pedicellate, inconspicuous; sepals 1.2–2.5 mm long, triangular, sparsely hirsute; petals white, equaling or slightly longer than the sepals; achenes 1.2–1.5 mm long, glabrous, grayish. Igneous gravel and sandy loam in sagebrush, grassland, and alpine tundra at 2745 to 3355 m in Piute, Sevier, and Wayne (?) counties; Alaska and Yukon east to Michigan and south to Colorado and North Dakota; Asia. Our materials are assignable to **var. *parviflora*** **(Nutt.) C. L. Hitchc.** [*Sibbaldia erecta* var. *parviflora* Nutt.); 4 (iv).

COLEOGYNE Torr.

Shrubs, the stems intricately branched, spinescent; leaves opposite, fasciculate on spur branchlets, entire, coriaceous, persistent; flowers perfect, regular, solitary and terminal on spur branchlets, subtended by paired, trifid bracts; hypanthium cup shaped, coriaceous, persistent; sepals 4, persistent; petals 0; stamens 20–40, basally inserted on outside of tubular sheath enclosing ovary; pistils 1, with a lateral, twisted, exserted, persistent style pubescent at base; fruit a glabrous achene.

Coleogyne ramosissima **Torr.** Blackbrush. Rounded shrubs, 3–12 dm or more tall, with divaricate branches; leaves 3–12 mm long, mainly 0.8–1.5 mm wide, narrowly oblanceolate, obtusish and commonly mucronate apically, strigose with malpighian hairs; sepals 4.5–6.5 (8) mm long, ovate to lanceolate, malpighian hairy and red brown dorsally, glabrous and yellowish ventrally; sheaths membranous, tapering to 5-toothed apex, silky-hairy within, glabrous without; achene ovate, curved, glabrous, 5–8 mm long. Shallow sandy to clay soils in blackbrush and warm desert and shrub communities at 760 to 1830 m in Emery, Garfield, Grand, Kane, San Juan, and Washington counties; Nevada and Colorado south to California and Arizona; 35(v).

COTONEASTER Medic.

Shrubs, unarmed, erect to arcuate or horizontal, deciduous or evergreen; leaves alternate, simple, entire; stipules linear, deciduous; flowers perfect, regular, solitary or in cymes terminating lateral branches; hypanthium short, persistent; sepals 5; petals 5, white or pink; stamens 10–20; pistil 1, the ovary inferior, 2- to 5-loculed, the styles 2–5; fruit a pome. **Note:** Members of this genus are cultivated widely in Utah as ornamentals. They have potential for use in reclamation and stabilization projects and will probably be maintained as a portion of our introduced flora. The genus has some 50 species distributed in Eurasia, and many more are in cultivation than are treated herein. The species keyed below are merely representative.

1. Leaves mainly 5–12 mm long; flowers usually solitary 2
— Leaves mainly 15–100 mm long or more; flowers commonly several to many 3
2(1). Petals spreading, white; shrubs spreading; leaves evergreen .... *C. microphylla* Lindl.
— Petals erect, pink; plants depressed-horizontal; leaves half evergreen .... *C. horizontalis* Decne.
3(1). Petals erect, obovate, pinkish or white; fruit red or black 4
— Petals spreading, suborbicular, white; fruit red 5
4(3). Fruit black; at least some leaves more than 2.5 cm long .... *C. acutifolia* Turcz.
— Fruit red; leaves less than 2.5 cm long .... *C. dielsiana* Pritz.
5(3). Leaves, glabrate at maturity .... *C. multiflora* Bunge
— Leaves persistent, white to rusty tomentose beneath 6
6(5). Leaves white-tomentos ebeneath, commonly 1–3 cm long .... *C. pannosa* Franch.
— Leaves rusty-tomentose beneath, or finally glabrate, often at least some over 3 cm long .... *C. salicifolia* Franch.

Note: *Cotoneaster* species are not described due to lack of adequate specimens in herbaria. Much work on cultivated plants is necessary.

COWANIA D. Don

Shrubs or small trees; leaves alternate, pinnatifid, coriaceous, glandular-dotted; stipules minute, triangular, persistent; flowers perfect, regular, solitary, terminal on spur branchlets; hypanthium funnelform, persistent; sepals 5; petals 5, white to cream or yellowish; stamens many; pistils 4–12 (commonly 5), long-hairy, the style terminal, plumose, persistent and elongate in fruit; fruit an achene.

Cowania mexicana **D. Don** Cliff-rose. Much branched shrubs or small trees, mainly 0.6–3.5 m tall with shreddy bark and glandular branchlets; leaves 3–15 mm long, cuneate-flabellate, mainly 5-lobed, glandular-punctate and green above, white-tomentose beneath; pedicels 2–8 mm long; sepals 4–6 mm long, ovate; petals 5–9 mm long, white to cream or yellowish; pistils commonly 5; styles plumose 2–6 cm long or more in fruit. Blackbrush, live oak, pinyon-juniper, ponderosa pine, desert peach, mixed grass-desert shrub, and mountain brush communities at 975 to 2745 m in Beaver, Box Elder, Carbon, Emery, Garfield, Grand, Juab, Kane, Millard, Salt Lake, San Juan, Sevier, Tooele, Utah, Washington, and Wayne counties; Nevada, Colorado, Arizona, California, New Mexico, and Mexico. Our materials belong to var. ***stansburiana*** (Torr.) Jeps. [*C. stansburiana* Torr.]. This species forms intergeneric hybrids with *Purshia tridentata* (q.v.). The problem has been investigated by Stutz and Thomas (1964. Evolution 18:183–195); 112(xxiv).

CRATAEGUS L.

Small, deciduous trees or shrubs, commonly armed with thorns; leaves alternate, simple, serrate to doubly serrate, lobed in some; stipules small, adnate to the petiole, glandular-serrate, deciduous; flowers perfect, regular, in corymbose cymes terminating short lateral branchlets; hypanthium short, free above the ovary; sepals 5, tardily deciduous; petals 5, white or pink; stamens (5) 10–25 or more, the filaments filiform; pistil 1, the ovary inferior, 1- to 5-loculed, the styles 1–5; fruit a pome. Only one taxon is widespread in Utah, growing as a portion of the indigenous flora. The following key contains other native and widely cultivated or escaping taxa. Others are present in cultivation but are excluded.

1. Leaves deeply 3- to 7-lobed; styles 1–3; fruits with 1 or 2 seeds; plants ornamental, cultivated and escaping .... *C. monogyna*

— Leaves serrate to doubly serrate or somewhat lobed; styles 2–5; plants indigenous 2

2(1). Leaves mostly more than twice as long as broad; plants common and widespread; fruit black .... *C. douglasii*

— Leaves mostly less than twice as long as broad; plants rare; fruit red, yellow, or orange 3

3(2). Petioles, at least some, with stalked red glands; teeth of leaves conspicuously tipped with reddish glands; plants known from Cache Co. .... *C. chrysocarpa*

— Petioles lacking stalked red glands; teeth of leaves not conspicuously red tipped; plants known from Provo Canyon .... *C. succulenta*

Crataegus chrysocarpa **Ashe** Yellow Hawthorn. (*C. rotundifolia* Moench, not Lam.; *C. doddsii* Ramaley). Shrub or small tree with rounded crown, 2–4 m tall or more with thorns 1–5 cm long or more; leaf blades 1.8–7 cm long, 1–7.2 cm wide, orbicular to obovate, acute apically, acute to broadly obtuse basally, the margins sharply doubly serrate (the serrations red tipped) and commonly lobed as well; petioles often glandular (at least some); inflorescence more or less villous at anthesis; sepals lance-attenuate to triangular, serrate; petals white, 6–8.5 mm long and about as broad; stamens 5–10; styles 2–4; fruit red to yellow-orange; "seeds" not pitted or deeply concave ventrally. Streamsides, reported from Cache Co. by Maguire (1937. Leafl. W. Bot. 2: 23–26); Alberta and Manitoba south to Colorado and Nebraska.

Crataegus douglasii **Lindl.** River Hawthorn. Shrubs or small trees, with rounded crowns, mainly growing as thickets, 2.5–5 (7) m tall, with thorns 1.2–3.5 cm long; leaf blades 1.3–9.5 cm long, 0.8–5.8 cm wide, lanceolate to elliptic, oblanceolate, or obovate, acute to obtuse apically, cuneate basally, serrate to doubly serrate, seldom lobed; petioles often with a pair of raised sub-basal glands; inflorescence glabrous; sepals triangular-attenuate, entire or serrulate, 1.5–3.5 mm long; petals white, 3–7.8 mm long and about as broad or broader; stamens 10–20; styles normally 5; fruit blackish, 6–12 mm thick. The species occurs from southeastern Alaska east to Michigan. Two rather well-defined varieties are present.

1. Petals 3–3.8 mm long, 2–4.2 mm wide; leaves slender, at least some 2–4 times longer than broad; fruit 6–8 mm thick when dried; plants of the Uinta Basin .... *C. douglasii* var. *duchesnensis*

— Petals 4.5–8 mm long, 5–7.8 mm wide; leaves commonly less than twice longer than broad; fruit 8–12 mm thick when dried .... *C. douglasii* var. *rivularis*

Var. ***duchesnensis*** **Welsh var. nov.** Similis *Crataego douglasii* var. *rivularis* sed differt in petalis breviore et angustiore foliis angustiore et pomis parviore. Type (in fruit). USA. Utah. Duchesne Co., Duchesne River valley, ca 24 Km northwest of Duchesne, along Utah Highway 35, Welsh, Atwood, and Moore 10928, 10 September 1970 (Holotype BRY). Additional specimens examined: Utah. Duchesne Co., Duchesne River valley, Erdman 2516, 17 August 1965; do, Rock Creek, 12 mi WNW of Mountain Home, Hansen s.n., 14 June 1976; do, 13 mi WNW of Mountain Home, Hansen s.n., 15 June 1976; do, T.1N., R.6W., Sec. 15, Hansen s.n., 14 June 1976; do, 5 mi NW of Hanna, Erdman 2522, 17 August 1965; Red Creek, ca 5 miles north of Fruitland, Brotherson 508, 21 June 1965. The Duchesne Hawthorn has long been recognized. It occurs along stream courses at 1800 to 2450 m in Duchesne and Uintah (?) counties; endemic; 8(ii).

Var. ***rivularis*** **(Nutt.) Sarg.** River Hawthorn. (*C. rivularis* Nutt. in T. & G.). Terraces, flood plains, alluvial fans and canal banks and other moist sites at 1370 to 2135 m in Box Elder, Daggett, Juab, Millard, Piute, Salt Lake, San Juan, Sanpete, Sevier, Summit, and Utah counties; Wyoming and Idaho (?) south to Arizona and New Mexico; 34(iv).

Crataegus monogyna Jacq. One-seeded Hawthorn. [*C. oxyacantha* var. *monogyna* (Jacq.) Loud.; *C. oxyacantha* L. nom. illeg.]. Shrub or small tree to 6 m tall, with thorns to 2 cm long; leaf blades 1.5–5.5 cm long and about as wide, broadly ovate to orbicular in outline, deeply 3- to 7-lobed, obtuse to truncate basally; petioles lacking glands; inflorescences glabrous to glabrate; sepals broadly triangular, 1.5–2.5 mm long; petals pink or white, 3–4 mm long, 4–5 mm wide; stamens commonly 20; styles 1 (2); fruit reddish or orange, 5.5–8 mm thick. Cultivated ornamental in Cache, Davis, Salt Lake, Utah, Weber, and perhaps in other counties, escaping in some; introduced from the Old World; 1 (0).

Crataegus succulenta Schrad. ex Link. Red Hawthorn. Shrubs or small trees, mainly 2–4 m tall with thorns to 4.5 cm long; leaf blades 1.8–7 cm long, 1–4.5 cm broad, elliptic to obovate, serrate to doubly serrate and often lobed; attenuate to cuneate basally, abruptly acuminate apically; petioles lacking glands; inflorescence sparingly villous to glabrate; petals white 5–7 mm long, 5.8–7.7 mm wide; stamens 10–20; styles 2–4; fruit red, 7–12 mm thick when dry. Indigenous in riparian habitats, mainly in Provo Canyon, Utah Co.; Colorado eastward to Pennsylvania and southeastern Canada; 3(i). **Note:** *Crataegus mollis* (T. & G.) Scheele and/or *C. crus-gallii* L. and perhaps other species of hawthorn occur in cultivation in Utah. The extent is not known at present.

CYDONIA Mill.

Small trees, unarmed; leaves alternate, simple, entire; stipules foliose, glandular margined, deciduous; flowers perfect, regular, solitary, terminal on leafy shoots; hypanthium short; sepals 5, persistent; petals 5, white or pale pink; stamens 15–20; pistils 1, the ovary inferior, commonly 5-loculed; styles 5; fruit a tomentose pome.

Cydonia oblonga Mill. Quince. (*Pyrus cydonia* L.; *C. vulgaris* Pers.). Trees to 6 m tall; leaves petiolate, the blades 1.1–9.5 cm long, 0.8–7 cm wide, ovate to ovate-oblong, villous-tomentose beneath, tomentose above when young, becoming glabrate; flowers solitary; sepals foliose, 6–9 mm long, tomentose (especially within), glandular margined; petals 13–25 mm long, 8–17 mm wide, obovate to obcordate, white to pale pink; fruit 6–10 cm in diameter, yellow, densely tomentose, fragrant, broadly pyriform. Cultivated ornamental and botanical curiosity in Utah and possibly other countries; introduced from the Middle East; 2 (0).

DRYAS L.

Shrubs or subshrubs, with stoloniferous branches; leaves alternate, simple, crenate to entire, sometimes incised at the base, evergreen; stipules narrowly lanceolate, adnate to the petiole, persistent; flowers perfect (rarely imperfect), regular, solitary; hypanthium saucer shaped, with an internal glandular disk; sepals 8–10, persistent; petals 8–10; stamens numerous; pistils numerous, distinct, the ovaries superior, each 1-loculed; styles 1 per pistil, much elongated in fruit; fruit an achene with a long-plumose style.

HULTEN, E. 1959. Studies in the genus *Dryas*. Svensk Bot. Tidskr. 5: 507–542.

PORSILD, A. E. 1947. The genus *Dryas* in North America. Canad. Field-Naturalist 61: 175–192.

Dryas octopetala L. Mat-forming shrubs; leaves petiolate, the petioles glabrous to sparingly villous and often glandular; leaf blades mostly 1–4 cm long, 0.3–1 cm broad, lanceolate to lance-oblong, obtuse apically, obtuse to subcordate basally, crenate, green and glabrous to pubescent above, tomentose below, commonly with stipitate glands on the midrib below, often revolute; scapes 1–11 cm long, tomentose and stipitate-glandular; petals white (fading yellowish) or rarely yellowish, 9–15 mm long; staminal filaments glabrous; styles plumose, in fruit to 4 cm long. Moraines, slopes, and ridge crests in alpine tundra and meadows at 3500–3965 m in Daggett, Duchesne, Summit, and Uintah counties; widespread in northern North America; circumboreal. Our material is assignable to var. **hookeriana** (Juz.) **Breitung** (*D. hookeriana* Juz.; *D. octopetala* ssp. *hookeriana* (Juz.) Hulten]; 9 (0).

EXOCHORDA Lindl.

Shrubs, deciduous, unarmed; leaves alternate, simple, entire or serrate; stipules none; flowers more or less imperfect (polygamo-dioecious), borne in terminal racemes; hypanthium flaring with a broad disk internally; sepals 5; petals 5, white; stamens 15–25; pistils 5, connate except for the 5 free styles, the ovary superior, 5-loculed; fruit a bony capsule.

***Exochorda racemosa* (Lindl.) Rehder** Pearl Bush. (*Amelanchier racemosa* Lindl.; *E. grandiflora* Hook.). Slender shrubs with spreading crowns, to 2.5 m tall or more, the herbage glabrous; leaf blades 1.2–6.5 cm long, 0.5–3.5 cm wide, elliptic to oblong or obovate, cuneate basally, mucronate apically, entire or some serrate in the upper half; racemes 3- to 10-flowered; flowers very showy; sepals 1–2 mm long, broadly rounded, erose apically, chartaceous; petals 10–17 mm long. Introduced ornamental in Utah County and in other low elevation urban areas; native to Asia; 2 (0).

FALLUGIA Endl.

Shrubs, deciduous, unarmed; leaves alternate, pinnately dissected; stipules adnate to the petiole, triangular-subulate, persistent; flowers mainly perfect, regular, terminal and solitary or in few-flowered cymes; hypanthium hemispheric, persistent, hairy within; sepals 5, alternating with slender bractlets; petals 5, white; stamens numerous; pistils numerous, the ovaries superior, of 1 carpel each; style terminal; fruit an achene, tipped by the plumose style.

***Fallugia paradoxa* (D. Don) Endl.** Apache Plume. (*Sieversia paradoxa* D. Don). Shrubs to 1.5 m tall, the herbage stellate hairy, the bark scaly; leaves mainly 4–16 mm long, cuneate-flabellate, 3- to 5-lobed, green and lepidote above, rusty-lepidote beneath; pedicels 2–18 mm long; sepals 4–7 (11) mm long, broadly ovate, abruptly acuminate-cuspidate apically; petals 11–14 mm long, 8–15 mm wide, white; pistils numerous; styles plumose, 2–4 cm long in fruit. Wash bottoms in mixed desert shrub and pinyon-juniper communities at 940 to 2290 m in Garfield, Iron, Kane, San Juan, Washington, and Wayne counties; Nevada and California east to Texas and south to Mexico; 32 (vii).

FRAGARIA L.

Herbaceous, rosulate perennials, commonly stoloniferous; leaves compound, with 3 serrate leaflets; stipules adnate to base of elongate petiole; flowers more or less imperfect (polygamo-dioecious), solitary, or in scapose cymes; hypanthium widely spreading; sepals 5, alternating with bractlets; petals 5, white or pinkish; stamens 20, sometimes abortive; pistils numerous, on a pulpy receptacle, superior; fruit of achenes, on a fleshy accessory receptacle.

Rydberg, P. A. 1908. *Fragaria.* N. Amer. Fl. 2: 356–365.

1. Petioles spreading-hairy; terminal tooth of leaflets relatively well developed, commonly surpassing the adjacent lateral teeth; inflorescence usually as long as or longer than the leaves .... *F. vesca*

— Petioles with hairs ascending to appressed-ascending; terminal tooth of leaflets small, commonly surpassed by the adjacent lateral teeth; inflorescence usually shorter than the leaves .... *F. virginiana*

***Fragaria vesca* L.** Starvling Strawberry. Stoloniferous herbs, with stems, petioles, and peduncles pubescent with slender spreading to somewhat ascending hairs; petioles 0.8–17.5 cm long (rarely longer); leaflets 3, the terminal one 1.3–6.5 cm long, 1–4.2 cm wide, thin, elliptic to oblong or obovate, coarsely serrate, silky pilose, subsessile or indistinctly petiolulate; scapes ultimately equaling or surpassing the leaves; cymes 3- to 15-flowered; sepals 3.5–7.2 mm long, acuminate to caudate; bracteoles 1.6–5.8 mm long, often bilobed; petals 5–10.5 mm long, white or pinkish; fruit to 1 cm thick, succulent, and palatable. Stream banks, terraces, and slopes, broad-leaved deciduous and coniferous woods and brushlands at 1800 to 3200 m in Box Elder, Cache, Carbon, Davis, Duchesne, Salt

Lake, San Juan, Sanpete, Summit, Tooele, Utah, and Weber counties; British Columbia and Alberta south to California and New Mexico. Our material is referable to **var. *bracteata*** **(Heller) R.J. Davis** [*F. bracteata* Heller; *F. vesca* ssp. *bracteata* (Heller) Staudt.; *F. helleri* Holz.]; 34 (ii).

Fragaria virginiana **Duchesne.** Mountain Strawberry. Stoloniferous herbs with stems, petioles, and peduncles with appressed to ascending hairs; petioles 2–15 cm long; leaflets 3, the terminal one 1.1–4.4 cm long, 0.5–2.2 cm wide, thickish, obovate to elliptic, coarsely serrate, silky pilose to glabrate, commonly petiolulate; scapes shorter than to surpassing the leaves; cymes 2- to 12-flowered; sepals 3.1–6.5 mm long; bracteoles 1.8–4.5 mm long, not or seldom bilobed; petals 3.5–10 mm long, white or rarely pinkish; fruit to 1 cm thick or more, succulent and palatable. Meadows, deciduous and coniferous woods at 2280 to 3300 m in Beaver, Duchesne, Emery, Garfield, Iron, Kane, Piute, Sanpete, Summit, Tooele, Utah, and Wayne counties; Alaska east to Northwest Territories and south to Colorado and California. Our material has been treated as belonging to two rather weak and intergrading varieties. The phase with large petals (i.e., more than 6 mm long) is supposedly more densely pubescent with spreading hairs. That phase is known as var. *platypetala* (Rydb.) Hall (*F. platypetala* Rydb.). It apparently intergrades completely with the small-flowered supposedly scantily pubescent phase with appressed hairs, known as var. *glauca* Wats. [*F. vesca* var. *americana* Rydb., not T.C. Porter; *F. glauca* (Wats.) Rydb.; *F. virginiana* ssp. *glauca* (Wats.) Staudt.]. In a broad sense, as herein interpreted, all of our material is best referred to a single taxon. The oldest available epithet appears to be **var. *glauca*** **Wats.**

GEUM L.

Perennial rhizomatous herbs; leaves alternate or opposite or mainly basal, pinnatifid to lyrate-pinnatifid; stipules foliose (at least on cauline leaves); flowers perfect, regular, solitary or in open cymes; hypanthium campanulate to saucer shaped; sepals 5, persistent, alternating with 5 bractlets; petals 5, usually yellow (sometimes pinkish or purplish); stamens numerous; pistils numerous, the ovaries superior, each 1-carpellate; style straight to bent or strongly geniculate and jointed, in some elongate in fruit and in some then with a deciduous terminal segment, in others plumose and persistent; fruit an achene.

1. Stems decidedly leafy; plants often more than 3.5 dm tall; sepals reflexed at anthesis; styles strongly geniculate and jointed, the persistent base hooked apically 2

— Stems subscapose; plants commonly less than 3.5 dm tall; sepals ascending to erect at anthesis; styles neither geniculate nor jointed 4

2(1). Persistent style base glandular-pubescent; terminal segment of basal leaves much larger than the lateral lobes, mostly rounded or subcordate at base; our common meadow and woodland *Geum* .... *G. macrophyllum*

— Persistent style base glabrous or hirsute, not glandular; terminal segment of basal leaves only somewhat larger than the lateral lobes, cuneate at base; plants uncommon 3

3(2). Petals equal to or shorter than the sepals; receptacle pubescent with coarse hairs; stem leaves with lobes or leaflets often about as broad as long, tapering to a rounded or acute apex; achenes about 70 .... *G. urbanum*

— Petals longer than the sepals; receptacle minutely hairy; stem leaves with lobes or leaflets distinctly longer than broad and mostly tapering to an acute apex; achenes 200 or more .... *G. aleppicum*

4(1). Cauline leaves opposite; petals white, pink, or only yellow tinged, erect or convergent; styles much elongate and plumose in fruit .... *G. triflorum*

— Cauline leaves alternate; petals yellow, spreading; styles about as long as the achene, glabrous .... *G. rossii*

Geum allepicum **Jacq.** Erect Avens. [*G. canadense* Murr., not Jacq.; *G. strictum* Ait.; *G. allepicum* var. *strictum* (Ait.) Fern.; *G. allepicum* ssp. *strictum* (Ait.) Clausen]. Plants shortly rhizomatous, 4.5–8 (10) dm tall, the stems and petioles spreading-hirsute; basal leaves 8–23 cm long, lyrate-pinnatifid, main lobes 5–9, all cuneate-obovate, strongly cleft and toothed, the terminal lobe larger but similarly shaped; cauline leaves several; flowers 2 to several; sepals soon reflexed, 4–8 mm long; petals yellow, spreading, about equaling the sepals; stamens 60 or more; achenes 3–4.5 mm long, tipped by persistent style; style strongly geniculate above the middle, the lower segment hirsute to glabrous, not glandular near the base, persistent and hooked apically. Wet to dryish meadows at 1400 to 2300 m in Grand, Summit, and Utah counties; widespread in North America and Eurasia; 3 (0).

Geum macrophyllum **Willd.** Large-leaved Avens. [*G. urbanum* ssp. *oregonense* Schintz; *G. oregonense* (Schintzl.) Rydb.; *G. macrophyllum* var. *rydbergii* Farw.]. Plants shortly rhizomatous, 2.3–11.5 dm tall, the stems erect, with spreading hairs; basal leaves 4–28 cm long or more, long-petiolate, the leaflets 9–25 or more, the apical lobe 2.5–13 cm long, 2–15 cm wide, acute to truncate or subcordate basally, dentate and conspicuously lobed, glabrate to glabrous above, hairy along the veins beneath; cauline leaves numerous; sepals 2.5–4.8 mm long, reflexed at anthesis; bracteoles 0.5–3.5 mm long, linear to lanceolate or lacking; petals yellow, 3–5.8 mm long; styles elongate with an s-shaped curve above the middle, glabrous or hairy above the bend, glandular (often sparingly so, or the glandular hairs deciduous) below the bend, hooked at apex, the apical section deciduous. Aspen, spruce-fir, birch-willow, and grass-sedge communities at 1280 to 2750 m in Box Elder, Cache, Carbon, Duchesne, Emery, Garfield, Kane, Piute, Salt Lake, Sanpete, Summit, Tooele, Uintah, Utah, Wasatch, and Washington counties; widespread in North America; Asia. Our materials, as described above, belong to a poorly differentiated variety, the **var.** ***perincisum*** **(Rydb.) Raup** [*G. perincisum* Rydb.; *G. macrophyllum* ssp. *perincisum* (Rydb.) Hulten]; 40 (vii).

Geum rossii **(R. Br.) Ser.** Ross Avens. [*Sieversia rossii* R. Br.; *Acomastylis rossii* (R. Br.) Greene]. Herbs, shortly rhizomatous, the rhizomes and stem bases with a persistent thatch of marcescent petioles and stems; stems 0.3–1.8 dm tall, erect, often with 1–3 greatly reduced leaves below the in florescence; basal leaves 2.2–12 cm long, short-petiolate, pinnatifid, with 15–31 entire to several-toothed or -lobed lateral divisions, the apical lobes similar to the lateral ones except smaller, glabrous to pubescent along veins below, ciliate; sepals 2.9–5.1 mm long, ovate to ovate-lanceolate; bracteoles 2–3.9 mm long, lanceolate; petals yellow, 6.4–8.6 mm long; styles straight, elongate, glabrous except at base, erect. Alpine meadows, rock stripes, and talus slopes at 3050 to 3400 m in Daggett, Duchesne, Juab, Piute, Salt Lake, Summit, Uintah, Utah, and Wayne counties; Alaska and Yukon south to Oregon, Nevada, Arizona, and New Mexico; Asia. The specimens from Utah are referable to var. ***turbinatum*** **(Rydb.) C. L. Hitchc.** [*Potentilla nivalis* Torr., not Lapeyr.; *G. turbinatum* Rydb.; *Sieversia turbinata* (Rydb.) Greene; *Acomastylis turbinata* (Rydb.) Greene; *G. sericeum* Greene; *S. sericea* (Greene) Greene], which is only weakly separable from the larger typical phase that occurs in the arctic; 14 (ii).

Geum triflorum **Pursh** Purple Avens; Old Man's Beard. [*Sieversia triflora* (Pursh) R. Br.; *Erythrocoma triflora* (Pursh) Greene; *G. ciliatum* var. *triflorum* (Pursh) Jeps.]. Plants shortly rhizomatous, clothed basally with persistent leaf bases; stems 1–4 dm tall, with 1–2 pairs of opposite leaves; basal leaves 2–18.5 cm long, pinnatifid, with mostly 15–31 cleft to lobed divisions, puberulent to pilose; flowers 1–7 (9); sepals showy, reddish to pink or purplish, 7–10 mm long; bracteoles linear to narrowly elliptic; petals yellowish to pink or suffused with crimson, 7–11.2 mm long; styles straight to moderately geniculate, plumose, 2–4 cm long at maturity. Oak-sagebrush, aspen, aspen-fir, and mixed conifer communities, often in meadows, at 1980 to 3500 m in Beaver, Daggett, Garfield, Iron, Sanpete, Sevier, Summit, and Wayne counties; British Columbia east to Newfoundland and south to Nevada, Arizona, New Mexico, Nebraska, and Illinois. Our specimens are assignable to the weakly differentiated var. **ciliatum (Pursh) Fassett** [*G. ciliatum* Pursh; *S. ciliata* (Pursh) D. Don; *Erythrocoma ciliata* (Pursh) Greene]; 20 (v).

***Geum urbanum* L.** Plants shortly rhizomatous, (3) 6–10 dm tall, the stems and petioles spreading-hirsute; basal leaves mainly 2–10 cm long, pinnatifid, the main lobes 3–5 (10), cuneate-obovate, rounded to acute at the apex, the terminal one rhombic-ovate and slightly larger than the lateral ones; cauline leaves several to many; sepals spreading to reflexed, 4–7 mm long; petals yellow, spreading, somewhat shorter than the sepals; achenes 3–6 mm long, tipped by the persistent style; style strongly geniculate above the middle. Disturbed sites, reported from Salt Lake County (Arnow 5546, UT), adventive from Eurasia; 0 (0).

HOLODISCUS Maxim. Nom. Cons.

Shrubs unarmed; leaves simple, alternate, toothed, deciduous; stipules lacking; flowers perfect, regular, each closely subtended by 1–3 bracteoles, numerous, borne in panicles; hypanthium saucer shaped, lined with a disk; sepals 5, persistent; petals 5, white to cream or less commonly pinkish; stamens about 20; pistils 5, the ovaries superior, each 1-carpellate; styles terminal, persistent; fruit a short-stipitate, villous achene.

LEY, A. 1943. A taxonomic revision of the Genus *Holodiscus* (Rosaceae). Bull. Torrey Bot. Club 70: 275–288.

***Holodiscus dumosus* (Nutt.) Heller** Mountain Spray. [*Spiraea dumosa* Nutt. in T. & G.; *S. discolor* var. *dumosa* (Nutt.) Wats.; *Schizonotus argenteus* var. *dumosus* (Nutt.) Kuntze; *H. discolor* var. *dumosa* (Nutt.) Dippel; *Schizonotus dumosus* (Nutt.) Koehne; *Schizonotus discolor* var. *dumosus* (Nutt.) Rehder; *Sericotheca dumosa* (Nutt.) Rydb.; *H. microphyllus* Rydb., type from Alta; *Sericotheca microphylla* (Rydb.) Rydb.; *H. discolor* var. *microphyllus* (Rydb.) Jeps.; *Sericotheca concolor* Rydb.]. Shrubs, densely to intricately branched, mainly 0.5–1.5 m tall; main foliage leaves on spur branches, the blades 0.5–3.2 cm long, 0.2–2.3 cm wide, obovate to oblanceolate or elliptic, cuneate basally, prominently toothed or lobed, villous to glabrate or glabrous on one or both surfaces, pale beneath; inflorescence 3–15 cm long; sepals 1.3–1.7 mm long, villous, sometimes pinkish; petals 1.9–2.2 mm long, white, cream, or pinkish; achenes somewhat flattened, villous-hirsute. Ubiquitous in numerous small plant communities, especially common on rock outcrops, slickrock plateau margins, and at bases of cliffs, or in talus slopes at 1280 to 3550 m in Beaver, Box Elder, Carbon, Davis, Duchesne, Emery, Garfield, Uintah, Utah, Washington, and Weber counties; Oregon east to Wyoming and south to California, Nevada, Arizona, and Mew Mexico. Attempts at recognition of infraspecific taxa are fraught with difficulties that are likely ecological rather than genetic reflections. A conservative approach is indicated; 60 (xii).

IVESIA T. & G.

Perennial herbs, from a caudex; leaves pinnately compound, alternate or primarily basal; stipules of cauline leaves foliose; flowers perfect, regular, borne in compact to open cymes; sepals 5, alternating with 5 bracteoles; hypanthium saucer to cup shaped, lined with a disk; petals 5, yellow or white; stamens 5 or 20; pistils 1–15, the receptacle hairy, the ovaries superior; style subterminal; fruit of achenes.

KECK, D. D. 1938. Revision of *Horkelia* and *Ivesia*. Lloydia 1: 75–142.

1. Leaflets usually fewer than 20; petals white to cream; plants of western Tooele Co. .... *I. baileyi*

— Leaflets commonly 22–80 or more; petals white or yellow; plants of various distribution 2

2(1). Petals white; stems more or less radiate-decumbent 3
— Petals yellow; stems erect or ascending 4
3(2). Stamens 5; hypanthium cup shaped; plants of Utah, Salt Lake, and Summit counties .... *I. utahensis*
— Stamens 20; hypanthium saucer shaped; plants of Beaver, Garfield, Sevier, and Tooele counties .... *I. kingii*
4(2). Hypanthium cup shaped; flowers in dense, congested cymes; plants widespread in central and northern Utah, our most common Ivesia .... *I. gordonii*
— Hypanthium saucer shaped; flowers in open cymes; plants of Beaver, Garfield, Kane, and Washington counties .... *I. sabulosa*

Ivesia baileyi* Wats.** Plants 0.4–2.5 dm tall, from a woody caudex clothed with persistent leaf bases; herbage glandular-pubescent; basal leaves 3.5–12 cm long; leaflets 10–20, 3–15 mm long, parted to divided; hypanthium disklike; sepals 2.5–3.2 mm long, ovate-lanceolate; bracteoles lance-oblong to ovate; petals white or cream, about equaling the sepals; stamens 5; pistils 3–7; styles glandular; achenes 1.6–2.3 mm long. Mountain slopes at 1700 to 3100 m in Tooele Co. (Deep Creek Mts.); eastern Nevada and adjacent Utah. Out material belongs to **var. *setosa Wats. [*Horkelia baileyi* var. *setosa* (Wats.) Rydb.; *I. setosa* (Wats.) Rydb.; *I. baileyi* ssp. *setosa* (Wats.) Keck]; 1(0).

***Ivesia gordonii* (Hook.) T. & G.** Gordon Ivesia. [*Horkelia gordonii* Hook.; *Potentilla gordonii* (Hook.) Greene]. Plants erect, 7–30 cm tall, from a thick woody caudex clothed with persistent leaf bases; herbage puberulent, glandular-puberulent, or glabrous; basal leaves 1–25 cm long; leaflets 20–50 or more, 2–17 mm long, divided to base; cymes congested, many-flowered, 1 or few or several; hypanthium campanulate; sepals 2–6.5 mm long, erect at anthesis, triangular-subulate; bracteoles 1.2–2.8 mm long; stamens 5; pistils 1–6; style not glandular; achenes 1.7–2.1 mm long. Ponderosa pine, spruce-fir, and mixed conifer woods and upwards in alpine sites, often in rocky meadows, at 2050 to 3660 m in Beaver, Davis, Duchesne, Morgan, Piute, Salt Lake, Sanpete, Sevier, Summit, Uintah, Utah, Wasatch, and Weber counties; Washington east to Montana and south to California and Colorado; 35(iv).

***Ivesia kingii* Wats.** King Ivesia. [*Potentilla kingii* (Wats.) Greene; *Horkelia kingii* (Wats.) Rydb.; *P. eremica* Cov.; *H. eremica* (Cov.) Rydb.; *P. kingii* var. *incerta* Jones; *I. halophila* Heller]. Plants decumbent, the stems 5–22 cm long, radiating from a thickened caudex clothed with blackish persistent leaf bases; herbage glabrous or pubescent, not glandular; basal leaves 0.5–12 cm long or more; leaflets 24–60 or more, 1–6 mm long, entire or ternately divided; cymes dichotomously divided, open; hypanthium saucer shaped; sepals 2.5–3.1 mm long, spreading at anthesis, lance-attenuate; bracteoles 1.3–1.9 mm long, ovate-lanceolate; petals white, 3–4.2 mm long, 2.5–3 mm wide, claws; stamens 20; pistils 2–9; styles not glandular; achenes 1.8–2.2 mm long. Saline meadows and pans at 1700 to 2380 m in Beaver, Garfield, Sevier, and Tooele counties; Nevada and California. The plants tend to blend with the pale substrate of the saline pans, perhaps accounting for the paucity of our records from Utah; 8(v).

***Ivesia sabulosa* (Jones) Keck** Sevier Ivesia. [*Potentilla sabulosa* Jones, types from head of Sevier River, "25 miles south of Panguitch"; *Comarella sabulosa* (Jones) Rydb.; *Horkelia sabulosa* (Jones) L. O. Williams; *H. mutabilis* Brandegee; *I. mutabilis* (Brandegee) Rydb.]. Plants erect, the stems 10–42 (50) cm tall, from a woody caudex clothed with persistent leaf bases; herbage glabrous to villous and glandular; basal leaves 3.5–23 (30) cm long, the petioles often suffused red purple; leaflets 30–80, paired, 1–13 mm long, usually divided to the base; cymes branched, open; hypanthium saucer shaped; sepals 3.3–5.5 mm long, triangular-acuminate, spreading at anthesis; bracteoles 1.3–2.7 mm long, lanceolate; petals yellow, 2.1–3 mm long, 0.3–0.5 mm wide; stamens 5; pistils 1–5; styles glabrous or nearly so; achenes 1.7–2.2 mm long.

Sagebrush, pinyon-juniper, pygmy sagebrush, ponderosa pine and spruce communities, commonly on limestone at 2050 to 2750 m in Beaver, Garfield, Kane, and Washington counties; Arizona (?) and Nevada. The type locality of *I. sabulosa* is recondite. Jones states (see Leafl. West. Bot. 10: 216. 1965) that "... And 4 miles below Ranch I got 6031 to 33f." The type of *I. sabulosa* is his number 6032. Jones further states that "Ranch is the name of the post office at the head of the Sevier and serves a little farming area there." Presumably "Ranch" and the collecting site are both in Garfield County; 7(iv).

Ivesia utahensis **Wats.** Utah Ivesia. [*Potentilla utahensis* (Wats.) Greene; *Horkelia utahensis* (Wats.) Rydb.] Plants decumbent or ascending, the stems radiating from a thickened caudex clothed with brownish leaf bases; herbage glandular-viscid or glandular-pubescent; basal leaves 1.2–9 cm long; leaflets 30–40, paired, 1–4 mm long, divided to base; cymes capitate, or in congested corymbs; hypanthium campanulate; sepals 1.5–2.7 mm long, narrowly triangular; bracteoles 1–1.3 mm long, oblong; petals white, 1.8–2.7 mm long, 1–1.7 mm wide; stamens 5; pistils commonly 2; styles not glandular; achenes 1.7–1.9 mm long. Alpine tundra and krumholz communities at 3200 to 3600 m in Salt Lake, Summit, Utah, and Wasatch counties; endemic; 3(0).

KERRIA DC.

Cultivated shrubs, unarmed, deciduous; leaves alternate, simple, doubly serrate; stipules lance-linear, deciduous; flowers perfect, regular, solitary, terminating short lateral branchlets of the current year; hypanthium short, lined by a disk; sepals 5, small, entire; petals 5, yellow; stamens numerous; pistils 5–8, the ovaries superior; style slender; fruit an achene (seldom produced).

Kerria japonica **(L.) DC.** Japanese Kerria. (*Rubus japonicus* L.) Shrubs with slender green arching branches; leaves 1–7 cm long, 0.7–3.5 cm wide, ovate to lanceolate, long-acuminate, bright green; pedicels 0.5–2.5 cm long; sepals about 3.5 mm long, broad-ovate, membranous; petals yellow, 12–20 mm long; achenes 4–5 mm long. Widely cultivated ornamental, persisting but not spreading, observed in Box Elder, Cache, Davis, Salt Lake, Utah, and Weber counties; introduced from Japan and China. Double flowered phases are common; 2(i).

MALUS Mill.

Trees with mainly unarmed branches; leaves alternate, simple, not or rarely lobed; stipules linear, caducous; flowers perfect, regular, borne in umbels; hypanthium short; sepals 5, persistent or deciduous; petals 5, white or pink; stamens usually 15–50; pistil 1, the ovary inferior, usually 5-loculed; styles 2–5, connate at the base; fruit variously shaped, applelike, the flesh usually lacking stone cells. **Note:** The apples are all introduced into our flora. Mostly they are cultivated and persist following cultivation, but they escape and are established widely in Utah, especially the pomological varieties. The following key is tentative; our cultivars often represent hybrid derivatives involving two to several of the species types. Other taxa are probably present in the state.

1. Leaves on elongated shoots lobed or notched; a crabapple .... *M. ioensis*

— Leaves on elongated shoots neither lobed nor notched 2

2(1). Mature leaves glabrous on both surfaces, serrate to crenate-serrate, but not sharply so; fruit mainly 1.5–2.5 cm in diameter; a crabapple .... *M. sylvestris*

— Mature leaves more or less tomentose on one or both surfaces, or if glabrous, then the pedicels very long and the fruit smaller 3

3(2). Pedicels 3–4.5 cm long, very slender; fruit mainly 0.8–1.2 cm in diameter; a crabapple .... *M. hupehensis*

— Pedicels mainly shorter than 3 cm long, slender to moderately thickened; fruit size various 4

4(3). Leaf margins sharply serrate; flowers ordinarily pink; flowering ornamental crabapple .... *M. floribunda*
— Leaf margins merely crenate-serrate to serrate; flowers various 5
5(4). Flowers commonly pink; fruit 0.8–1.2 cm in diameter; a crabapple .... *M. baccata*
— Flowers commonly white within (pink sometimes on dorsal surface) .... *M. pumila*

***Malus baccata* (L.) Borkh.** Siberian Crab. [*Pyrus baccata* L.]. Small trees to 5 m, the branchlets glabrous; leaves ovate to oblong, 2–8 cm long, serrate, glabrous to puberulent on one or both sides; petioles 1.5–5 cm long; petals white or pink, 12–18 cm long; fruit 0.8–1.2 cm in diameter, the calyx deciduous. Cultivated ornamental tree in lower elevation portions of Utah; introduced from Asia; 4 (0).

***Malus floribunda* Sieb. ex Van Houtte** Showy Crab. [*Pyrus floribunda* Sieb.]. Small trees to 8 m, the branchlets pubescent; leaves ovate to oblong, 2–7 cm long, sharply serrate, usually tomentose on one or both sides; petioles mostly 1.5–5 cm long; petals rose pink, 15–20 mm long or more; fruit mostly 0.5–1 cm in diameter. Cultivated ornamental trees in lower elevation portions of Utah; introduced from Japan; 5 (0).

***Malus hupehensis* (Pamp.) Rehder** Tea Crab. [*Pyrus hupehensis* Pamp.; *M. theifera* Rehder]. Small trees to 5 m tall, the branchlets glabrous or essentially so; petioles 0.8–4 cm long; leaf blades oblong-elliptic to ovate, 2.5–7.8 cm long, minutely tomentulose on both sides at maturity; peduncles 3–4.5 cm long; sepals 4–6 mm long; petals 15–20 mm long, commonly white; fruit 0.8–1.2 cm in diameter. Cultivated ornamental trees of lower elevations in Utah; introduced from Asia; 7 (0).

***Malus ioensis* (Wood) Britt.** Iowa Crab. [*Pyrus ioensis* (Wood) Bailey]. Small trees to 9 m tall, the branchlets tomentose; leaves ovate to oblong, 2.5–10 cm long, tomentose on both sides at least when young; petals usually white (sometimes pinkish), 12–25 mm long; fruit 2–3 cm in diameter. The Iowa crab is grown occasionally in lower elevation portions of Utah; introduced from the north central states; 4 (0).

***Malus pumila* Mill.** Common Apple. [*M. domestica* Borkh.]. Small to moderate trees to 10 m tall, the branchlets tomentose when young, becoming glabrous; leaves ovate to oblong or elliptic, 1.5–10 cm long, tomentose on one or both sides (even in age); petals usually white within, often pink dorsally, 12–25 mm long; fruit mainly 2.5–12 cm in diameter, red, reddish purple, or yellow. This is the apple of commerce, and it is widely cultivated in Utah; it persists and occurs as established trees throughout the state; introduced from Eurasia; 18 (ii).

***Malus sylvestris* Mill.** Crabapple. Small to moderate trees to 10 m tall, the branchlets glabrous or puberulent when young, often somewhat thorny; leaf blades 2–6 cm long, ovate to elliptic, crenate-serrate, acuminate or cuspidate; petals 8–20 mm long, white or pink; fruit mainly 1.5–2.5 cm in diameter, sour. Introduced cultivated trees, persisting and escaping in Utah; native to Eurasia; 6 (1).

PERAPHYLLUM Nutt. in T. & G.

Shrubs, unarmed, deciduous; leaves alternate, simple, entire or nearly so; stipules adnate to petioles, triangular, minute, deciduous; flowers perfect, regular, solitary or few on lateral branchlets of the season; hypanthium campanulate, disk lined; sepals 5, spreading to reflexed, persistent; petals 5, white or pink; stamens 15–20; pistil 1, the ovary inferior, 2- to 3-carpellate but falsely 4- to 6-loculed by intrusion of parietal septa; styles 2 or 3, the stigma capitate; fruit a fleshy apple-like pome.

***Peraphyllum ramosissimum* Nutt. in Torr. & Gray.** Squaw-apple. Shrubs 4–15 (20) dm tall, intricately branched; leaves alternate, mainly on short lateral spurs, 1.1–3.9 cm long, 0.4–0.9 cm wide, oblanceolate, abruptly acute, appressed puberulent (especially beneath), entire or minutely serrulate; pedicels 4–13 mm long, with 1–3 caducous bractlets; sepals 2.9–4 mm long, triangular-acuminate, serrulate to entire; petals white to pink, 6.5–9 mm long, 5–8.5 mm wide; pomes 8–18 mm thick, yellow orange, the flavor bad when ripe. Oak-sagebrush, pinyon-juniper, mountain brush, and ponderosa pine communities at 1500 to 2500 m in Beaver, Garfield, Grand, Juab, Kane, Millard, San Juan, Sanpete, Sevier, and Washington counties; Oregon and Idaho south to California and Colorado. The fruit is attractive when ripe but the flavor is not agreeable. Perhaps, when cooked with sugar it might be better?; 20 (vi).

PETROPHYTUM (Nutt.) Rydb.

Shrubs, prostrate and mat forming, conforming to the rock substrate; leaves alternate, commonly appearing rosulate, simple, entire, stipules lacking; flowers perfect, regular, borne in compact spikelike panicles on scapose, bracteate peduncles; pedicels with 1 or more bractlets; hypanthium cup shaped, lined with a disk; sepals 5, erect at anthesis; petals 5, white; stamens numerous; pistils commonly 5, the ovaries superior, each 1-loculed; styles slender, exserted from the flower; fruit of usually 5 follicles.

***Petrophytum caespitosum* (Nutt.) Rydb.** Rock Spiraea. [*Spiraea caespitosa* Nutt. in T. & G.; *Eriogyna caespitosa* (Nutt.) Wats.; *Luetkea caespitosa* (Nutt.) Kuntze]. Mat-forming shrubs to 10 dm broad or more; leaves 3–17 mm long, 1.5–4.5 mm wide, spatulate to oblanceolate or obovate, pilose on one or both surfaces, rarely almost or quite glabrous; peduncles 0.5–12 cm long, with bractlike leaves much reduced upwards; panicles spikelike, 0.5–2.5 cm long, often branched at base or with axillary panicles along axis of peduncle; pedicels 0.5–3 mm long, bracteolate; sepals 1.2–2.1 mm long, narrowly triangular; petals 1.3–2.5 mm long, 0.4–0.8 mm wide, white; fruit 1.5–2.1 mm long. On limestone or granitic outcrops or gravels from sagebrush upwards to spruce-fir communities and on sandstone (Entrada, Navajo, Kayenta, Cedar Mesa, etc.) often in hanging gardens at lower elevations (1000 to 2750 m) in Beaver, Cache, Grand, Juab, Kane, Millard, Utah, and Washington counties; Oregon east to South Dakota and south to California, Arizona, New Mexico and Texas. This beautiful dwarf shrub flowers in late summer and autumn. Major variations involve the tendency to glabrous leaves of some Great Basin specimens, and a tendency to short peduncles in some materials from the hanging gardens of southeastern Utah. More materials are required to adequately assess the variation; 25 (vii).

PHYSOCARPUS Maxim. Nom. Cons.

Shrubs, unarmed, deciduous, with exfoliating bark; leaves alternate, simple, palmately lobed and veined, usually with at least some stellate hairs; stipules membranous, deciduous; flowers perfect, regular, borne in terminal corymbs; hypanthium cup shaped, lined with a disk; sepals 5; petals 5, white or pink; stamens 20–40, inserted with petals at edge of disk; pistils 1–5, the ovaries superior and partially connate; styles slender, the stigmas capitate; fruit of one or more follicles, each several seeded.

HOWELL, J. T. 1931. A Great Basin species of *Physocarpus*. Proc. Calif. Acad. Sci. IV. 20:129–134.

1. Pistil and style solitary; leaves less than 2 cm long; staminal filaments of two alternating and markedly unequal lengths .... *P. alternans*
— Pistils and styles 2 or 3, or the carpels connate below; leaves various but commonly over 2 cm long; staminal filaments subequal or somewhat unequal 2
2(1). Leaves mainly 0.7–2.5 cm long; mature carpels swollen, not flattened; plants evidently rare in Utah .... *P. monogynus*
— Leaves mainly 2–8 cm long; mature carpels flattened; plants common in south central to northern Utah .... *P. malvaceus*

***Physocarpus alternans* (Jones) J. T. Howell** Dwarf Ninebark. [*Neillia monogyna* var. *alternans* Jones; *Opulaster alternans* (Jones) Heller] Shrubs commonly 4–12 dm tall, and about as broad; twigs stellate pubescent and sometimes glandular; bark shreddy on older twigs; leaf blades 0.3–2 cm long, 0.3–2.2 cm wide, oval-ovate to ovate, cordate to subcordate basally, more or less 3-lobed, doubly crenate, pubescent to sparingly pubescent on both sides; inflorescence subumbellate, (1) 2- to 12 (17) -flowered; pedicels 2–10 mm long; hypanthium stellate-hairy; sepals 1.3–3.2 mm long, oval to suboblong; petals 1.8–3.2 mm long, 1.5–3 mm wide, white or suffused with red pink; follicle solitary, densely stellate, 4–5 mm long. Rock outcrops, ledges, and cliff faces in desert shrub, pinyon-juniper, oak, and ponderosa pine communities at 1980 to 2750 m in Daggett, Duchesne, Emery, Garfield, Millard, San Juan, Utah, Wayne, and Washington counties; Idaho, Nevada, and Colorado. Jones (Zoe 4:38–44. 1893) discussed the problems within the genus *Physocarpus* then called *Niellia*. The basic problems are still as Jones outlined them eight decades ago. The genus is still in need of a definitive revision; 14(iv).

Physocarpus malvaceus **(Greene) Kuntze** Mallow-leaved Ninebark. [*Niellia malvacea* Greene; *Opulaster malvaceus* (Greene) Kuntze; *N. monogyna* var. *malvacea* (Greene) Jones; *Spiraea opulifolia* var. *pauciflora* T. & G.; *Opulaster pubescens* Rydb.; *O. cordatus* Rydb.] Shrubs, mainly 8–20 dm tall, rarely more, and often as broad; twigs glabrous to minutely stellate; bark shreddy on older branchlets; leaf blades (0.8) 2.2–8 cm long, (1.2) 2–8.2 cm wide, ovate to broadly ovate, cordate basally, 3-lobed, doubly crenate, glabrous above, stellate-pubescent to glabrous beneath; inflorescence corymbose, 5- to 30(+)-flowered; pedicels 0.7–2.3 cm long; hypanthium stellate-hairy; sepals 2.2–4.6 mm long, ovate to lance-oblong; petals 3.3–6.7 mm long, 1.5–4.8 mm wide, white; follicles paired, connate to the middle or above, substipitate, densely stellate, 4.9–6 mm long. Moist slopes and streamsides in mountain brush, aspen, and mixed conifer woodlands at 1600 to 3300 m in Cache, Emery, Garfield, Juab, Millard, Salt Lake, Sanpete, Summit, Tooele, Utah, Wasatch, and Weber counties; British Columbia east to Alberta and south to Oregon, and Wyoming; 39(vii). Two other large-leaved ninebark species are known from cultivation in Utah. They are *P. opulifolius* (L.) Raf. (*Spiraea opulifolia* L.) and *P. capitata* (Pursh) Kuntze (*Spiraea capitata* Pursh). They both possess 3–5 glabrous pistils connate only at the base. They differ in that the leaves of *P. opulifolius* are commonly glabrous beneath and those of *P. capitatus* are ordinarily densely stellate beneath. The extent of these species in cultivation is not known.

Physocarpus monogynus **(Torr.) Coult.** Mountain Ninebark. [*Spiraea monogyna* Torr.; *Opulaster monogynus* (Torr.) Kuntze]. Shrubs, mainly 4–20 dm tall; twigs glabrous to densely stellate; bark shreddy on older branchlets; leaf blades 0.5–2.8 cm long, 0.6–3.2 cm wide, ovate to orbicular, cordate basally, commonly 3-lobed, doubly crenate, glabrate or glabrous on both sides or sometimes stellate hairy especially below; inflorescence corymbose, 9- to 25-flowered (sometimes more); pedicels 0.3–0.8 cm long; hypanthium stellate-hairy; sepals 2.3–3 mm long, ovate; petals 2.2–3.9 mm long, 2.6–3.5 mm wide, white; follicles paired, connate to the middle or above, substipitate, densely stellate; 3–4.5 mm long. Canyon bottoms and moist slopes in mountain brush, aspen and Douglas fir communities at 1650 to 2150 m in Carbon and Utah counties; South Dakota and Wyoming south to Texas and Arizona (?); 2 (i). Our material seems to fit well within the range of variation of materials from Colorado, New Mexico, and South Dakota. The plants are smaller in all features from the similar *P. malvaceus* (q.v.).

POTENTILLA L.

S. L. Welsh & B. C. Johnston

Annual, biennial, or perennial herbs (a shrub in *P. fruticosa*); leaves alternate or basal, palmately or pinnately compound; stipules lanceolate to ovate, sometimes sheathing; flowers perfect, regular, borne solitary or in cymes; hypanthium saucer shaped to cup shaped; sepals 5, alternating with bractlets; petals 5, yellow to ochroleucous (fading white in some), broadly obovate and often emarginate; stamens 10–25; pistils numerous, on a hemispheric to conical receptacle, superior; fruit of achenes, the styles terminally, medially, or basally attached, jointed, finally deciduous, glabrous or papillose. **Note:** This is a fairly difficult genus, with many interpretations, due partially to hybridization, which obscures differences between taxa, and because of different weight given to portions of the genus as providing basis of segregation into several genera. We have resisted segregation of the Utah species into the genera *Argentina*, *Drymocallis*, and *Pentaphylloides*. These generic names will be used by some authors, nevertheless, and we have included the designations for them in the following key. These names, as synonyms, are provided in the body of the treatment.

HITCHCOCK, C. L. 1961. Rosaceae. *In* C. L. Hitchcock, A. Cronquist, M. Ownbey, and J. W. Thompson. Vascular Plants of the Pacific Northwest. Univ. Washington Publ. Biol. 17(3): 89–194.

KECK, D. D. 1940. *Potentilla glandulosa* and its allies: taxonomy. *In* J. Clausen, D. D. Keck, and W. M. Hiesey. Environmental studies on the nature of species. I. Effect of varied environments on western north American plants. Carnegie Inst. Washington Publ. 520: 31–49. *Potentilla gracilis* and its allies, *op. cit.*, pp. 128–137.

LEHMANN, J. C. G. 1856. Revisio Potentillarum Iconibus Illustrata. Verh. Kaiserl. Leopold Akad. Vol. 23. suppl.

RYDBERG, P. A. 1898. Monograph of the North American Potentillae. Mem. Dept. Bot. Columbia Univ. No. 2.

______. 1908. Potentilleae. N. Amer. Fl. 22(¾): 268–377.

______. 1922. Flora of the Rocky Mountains and Adjacent Plains. New York, by the author, ed. 2.

TIDESTROM, I. 1925. Flora of Utah and Nevada. Contr. U.S. Natl. Herb. 25: 1–665.

WOLF, T. 1908. Monographie der Gattung *Potentilla*. Bibliotheca Botanica 16(71).

1. Plants woody shrubs; styles laterally attached to the ovary; ovaries and achenes hairy (*Pentaphylloides* Duham.) .... *P. fruticosa*

— Plants herbaceous; styles basal, terminal, or lateral; ovaries and achenes glabrous 2

2(1). Plants strongly stoloniferous; styles laterally attached to the ovary; leaves evidently pinnate, strongly bicolored, silvery white beneath (*Argentina* Lam.) .... *P. anserina*

— Plants without stolons, or rarely somewhat stoloniferous; styles basal or terminal; leaves usually not evidently pinnate and strongly bicolored 3

3(2). Styles basally attached to the ovary, relatively short (ca 1 mm) and deltoid, gradually tapering upward from the flaring base; plants medium to tall, with pinnate leaves and often flabellate leaflets (*Drymocallis* Lam.) 4

— Styles terminal, sometimes short, but not deltoid, if thickened at base then abruptly tapered; plants prostrate, short, or tall; leaves pinnate to palmate (*Potentilla* L., sens. str.) 6

4(3). Leaflets 9–11, usually dark green, deeply and sharply toothed, often with interspersed smaller leaflets between paired ones; stems often stoloniferous, less than 30 cm tall; flowers creamy white; plants rare .... *P. fissa*

— Leaflets 5–9, usually lacking interspersed smaller leaflets; stems and leaves medium to pale green, larger; flowers yellow to white 5

5(4). Inflorescence short and dense, capitate, with erect branches; stem stout, often densely brown-villous; petals creamy white, about equaling the sepals; plants mostly 40 cm tall or more; plants uncommon .... *P. arguta*

— Inflorescence open, with diverging branches, or if dense then the stems neither stout nor villous; petals cream to yellow; plants mostly less than 40 cm tall; plants common .... *P. glandulosa*

6(4). Stems branched at or below the middle, the basal leaves lacking and midstem leaves developed at anthesis; styles to 1 mm long, conspicuously thickened at base; plants annual or short-lived perennials, of damp disturbed sites 7

— Stems usually branched above the middle, the basal leaves persistent at anthesis, the midstem leaves reduced; style 0.8–4.5 mm long, thickened at base or not; plants perennial 11

7(6). Leaves conspicuously white, tomentose beneath, small, palmate, dissected into narrow lobes; plants adventive, to be expected in Utah .... *P. argentea* L.

— Leaves not tomentose, strigose and often glandular, palmate or pinnate 8

8(7). Leaves all apparently pinnately compound, with 5–7 leaflets; achenes with a thickened appendage on inner margin .... *P. paradoxa*

— Leaves (at least the uppermost) ternate or palmate, or if the lowermost ones pinnate then leaflets crowded and subpalmate; achenes without an appendage 9

9(8). Lowermost leaves crowded-pinnate or subpalmate, with 5–7 leaflets; stems and calyx without glandular or pustulate hairs .... *P. rivalis*

— Lower leaves ternate or palmate; stems and calyx glandular or hirsute with pustulate hairs 10

10(9). Stems covered with glandular hairs; leaves all ternate; petals often shorter than the sepals .... *P. biennis*

— Stems with pustulate, spreading, stiff-hirsute hairs, and sometimes also with few glandular hairs; leaves ternate to palmate; petals often equaling sepals .... *P. norvegica*

11(6). Style to 1 mm long, often thickened at base, relatively thick just below the stigma; leaves tomentose, at least below 12

— Style 1.2 mm long or more, usually over 1.5 mm, often narrow just below the stigma 16

12(11). Leaves ternate, or less commonly 5-foliolate, or subpalmate, snowy white-tomentose beneath, the margins usually plane; inflorescence open; calyx usually lacking glands; plants alpine 13

— Leaves pinnate, or less commonly subpalmate, olive greenish or yellowish-tomentose beneath, the margins usually revolute; inflorescence glomerate, compact; calyx glandular; plants variously distributed .... *P. pensylvanica*

13(12). Leaves subpalmate, with 5 leaflets; petioles strigose and tomentose; styles conelike, conspicuously thickened and papillose at base 14

— Leaves ternate; petioles strigose and tomentose, or only tomentose; styles uniformly thickened, or sometimes only somewhat thickened below the stigma, rarely thickened at base 15

14(13). Leaves somewhat subpalmate, the rachis very short (ca 5–15 percent of petiole length), conspicuously strigose on petioles and on both surfaces .... *P. rubricaulis*

— Leaves subpalmate to subpinnate, the rachis longer (ca 20–40 percent of petiole length), tomentose beneath .... *P. nivea* x *P. pensylvanica* var. *paucijuga*

15(13). Petioles strigose and tomentose; pubescence snow white to off-white; plants often more than 10 cm tall, rare in the Deep Creek, La Sal, and Uinta mountains. .... *P. hookeriana*

— Petioles tomentose only; pubescence snow white; plants commonly less than 10 cm tall, rare, alpine, in La Sal Mountains. .... *P. nivea*

16(11). Leaves palmate to subpalmate, not pinnate 17

— Leaves pinnate 22

17(16). Upper leaf surfaces and calyx glandular, often also strigose; stems to 15 cm long (rarely more), prostrate-ascending 18

— Upper leaf surfaces and calyx glabrous, sericeous, or tomentose; stem length various, but usually over 15 cm long 19

18(17). Petioles to 5 cm long; leaflets usually bicolored, tomentose beneath, strigose (at least) above; sepals and bractlets relatively broad, usually deltoid; styles 1.6–2.4 mm long, sometimes clavate; plants widespread .... *P. concinna*

— Petioles usually over 5 cm long; leaflets strigose on both surfaces, not bicolored; sepals and bractlets narrow, acuminate; styles 2.1–3 mm long, filiform .... *P. multisecta*

19(18). Leaves bicolored, tomentose beneath; leaflets 7–9, palmate or subpalmate, short-serrate below middle, ovate or obovate; style filiform, if thickened, then slightly so at base .... *P. pulcherrima*

— Leaves not bicolored, or only slightly so, if tomentose beneath then not densely so and the leaflets oblanceolate or dissected almost to midrib; leaflets 5–7, palmate to subpalmate, not toothed below the middle in some; style filiform or uniformly thickened 20

20(19). Leaflets toothed above the middle, cuneate, never bicolored, green to grayish green; anthers mostly 0.5–0.7 mm long; stems decumbent to ascending; plants alpine or subalpine .... *P. diversifolia*

— Leaflets toothed to below the middle, often bicolored and pale beneath; anthers 0.8–1.3 mm long; stems ascending to erect 21

21(20). Leaflets divided two-thirds or more to midrib into linear segments, or some segments more than 5 mm long, whitish or grayish beneath .... *P. pectinisecta*

— Leaflets divided to one-half the distance to midrib, the teeth les than 5 mm long, usually green or greenish on both surfaces .... *P. gracilis*

22(16). Leaflets tomentose, at least below, rarely strigose or glandular; stems usually ascending, 20–60 cm tall; leaflets sometimes confluent with rachis; plants of montane to subalpine 23

— Leaflets seldom tomentose, or if so then sericeous, strigose or glandular; stems decumbent to ascending, 5–35 cm tall, or if taller then leaflets strigose and glandular; leaflets not confluent with rachis; plants of submontane, montane, or alpine sites 24

23(22). Calyx densely tomentose at anthesis, with dark bractlets much smaller than the lobes; leaflets tomentose above, not strongly bicolored, 9- to 19-toothed; stems leafy; plants of the Uinta Mts. .... *P. effusa*

— Calyx sericeous at anthesis, the bractlets similarly colored and subequal to the lobes; leaflets various above, often strongly bicolored, 13- to 37-toothed; stems not leafy; plants widespread .... *P. hippiana*

24(22). Leaflets strigose and usually also glandular beneath sometimes also tomentose above; pedicels straight; inflorescence branches divaricate; plants of south central Utah .... *P. crinita*

— Leaflets glabrous to sericeous, if strigose (as rarely) then plants with recurved pedicels; inflorescence open, but branches not divaricate; plants mainly of northern Utah 25

25(24). Pedicels recurved in fruit; lower leaflets conspicuously pinnately toothed; stems decumbent or spreading; plants rare, in wet meadows .... *P. platensis*

— Pedicels straight or ascending in fruit; lower leaflets pinnately toothed or apically few toothed; stems decumbent to ascending; plants montane to alpine .... *P. ovina*

Potentilla anserina **L.** Common Silverweed. [*Argentina anserina* (L.) Rydb.; *A. argentea* Rydb.; *P. anserina* var. *grandis* T. & G.; *A. anserina* var. *grandis* (T. & G.) Rydb.; *P. egedii* var. *grandis* (T. & G.) Howell; *P. pacifica* Howell; *A. pacifica* (Howell) Rydb.]. Perennial herbs, with long strawberrylike stolons; leaves 2–100 cm long or more, pinnately compound with 5–25 main leaflets interspersed by smaller ones, the terminal leaflet 0.5–5.5 cm long, 0.3–2.6 cm wide, oval to oblong or oblanceolate to obovate, coarsely serrate, green and glabrous to pilose above, pale and villous over a tomentum beneath; scapes 1.5–15 cm long or more, villous to densely so, leafless; sepals ovate, 3–10 mm long, pubescent to glabrous, erect, enlarging in fruit; petals yellow, 7.5–16 mm long; achenes 1.5–2 mm long. Meadows, lake shores, terraces, and floodplains, especially where wet part of the season, at 1300 to 2600 m in Carbon, Garfield, Kane, Millard, Piute, Salt Lake, Sanpete, Sevier, and Utah counties; widespread in North America; circumboreal. The worldwide review by Rousi (Ann. Bot. Fenn. 2: 47–112. 1965) indicates that formal varieties are not warranted; 24 (ii).

Potentilla arguta **Pursh** Acute Cinquefoil. (*P. pensylvanica* var. *arguta* (Pursh) Ser. in DC.; *P. agrimonioides* var. *arguta* (Pursh) Farw.; *Drymocallis arguta* (Pursh) Rydb.; *Geum agrimonioides* Pursh; *P. agrimonioides* (Pursh) Farw., not Beib.; *D. agrimonioides* (Pursh) Rydb.; *P. convallaria* Rydb.; *D. convallaria* (Rydb.) Rydb.; *P. arguta* var. *convallaria* (Rydb.) T. Wolf; *D. corymbosa* Rydb.) Perennial, glandular-pubescent herbs, 2.5–6 (8) dm tall, from a caudex; basal leaves 6–30 mm long, pinnately compound with 5–11 leaflets, the terminal one 15–60 mm long (or more), 12–40 mm wide, oval to elliptic or obovate, doubly dentate to somewhat lobed, green and glandular-pubescent on both surfaces; flowers several to many, showy; sepals 4–8 mm long, lance-ovate, longer in fruit; bracteoles 2–6 mm long, oblong to narrowly lanceolate; petals yellow to cream or white, mostly 5–8 mm long; receptacle sparsely hairy; achenes 1–1.5 mm long; styles basal, ca. 1.0 mm long, deltoid. Mountain brush, aspen, and spruce-fir communities, often in meadows, at 1950 to 3360 m in Davis, Juab, Salt Lake, San Juan, Sanpete, Summit, Utah, Washington (?), and Weber counties; the species is widespread in North America. Our material is referable to var. ***convallaria*** **(Rydb.) T. Wolf**, and is transitional to *P. glandulosa* (q.v.); 14 (i).

Potentilla biennis **Greene** Green Cinquefoil. [*Tridophyllum bienne* (Greene) Greene; *P. lateriflora* Rydb., type from Utah; *P. kelseyi* Rydb.] Annual or biennial herbs, mostly 1–6 (7) dm tall, from taproots; leaves mainly cauline, palmately 3 (4) -foliolate, the terminal leaflet 1–5 cm long, 1–3 cm wide, obovate to oblanceolate, crenate-serrate, pubescent with spreading to appressed hairs and multicellular glandular ones; flowers several to numerous, inconspicuous; sepals mostly 2–4 mm long, ovate to lance-ovate; bracteoles 2–3 mm long, ovate-lanceolate to oblong; petals yellow, 1.5–3 mm long; achenes numerous, about 1 mm long; styles terminal, ca. 1.0 mm long, basally thickened. Meadows, streamsides, springs, and seeps at 1525 to 2324 m in Beaver, Duchesne, Garfield, Iron, Salt Lake, Sevier, Wasatch, and Washington counties; widespread in western North America; 7 (v).

Potentilla concinna **Richards.** Pretty Cinquefoil. Perennial herbs, the stems decumbent-spreading to ascending, 0.1–1 dm tall; leaves mainly basal, palmately to pinnately 5- to 7 (9) -foliolate, the terminal leaflet 0.3–3.8 cm long, 0.1–1 cm wide, obovate to oblanceolate, toothed only at apex or along the length, often folded, not markedly bicolored, pilose and tomentose beneath, pilose to glabrous (less commonly tomentose) above; cauline leaves 1 or 2; cymes (1) 2- to 7-flowered, the flowers showy; sepals 2.2–4.8 mm long, triangular-ovate; bracteoles 1.3–3.5 mm long, oblong to lanceolate; petals yellow, 2.7–7.3 mm long; achenes numerous, 1.6–2 mm long; style subapically attached, smooth or glandular, not basally thickened, sometimes clavate. Three rather weak varieties are present in Utah, separable as follows:

1. Leaflets pinnately disposed, often 7, the lowermost often scattered or reduced; stems usually trailing, longer than basal leaves; pubescence translucent-brownish; plants of western Utah .... *P. concinna* var. *proxima*

— Leaflets palmately disposed, commonly 5–9; stems shorter than basal leaves; pubescence white 2

2(1). Leaflets toothed from the middle or below (at least some), commonly flat and green above; plants widespread .... *P. concinna* var. *modesta*

— Leaflets toothed at apex only, rarely minutely crenate also, commonly folded, the obscured upper surface greenish or not .... *P. concinna* var. *bicrenata*

Var. *bicrenata* (Rydb.) Welsh & Johnston, comb. nov. [based on: *Potentilla bicrenata* Rydb. Bull. Torrey Bot. Club 23: 431. 1896]. Pinyon-juniper, grassland, sagebrush, ponderosa pine, and spruce-fir communities at 2050 to 2875 m in Beaver, Duchesne, Emery, Garfield, San Juan, Sevier, and Wayne counties; Colorado, Wyoming, and New Mexico; 14 (ii).

Var. *modesta* (Rydb.) Welsh & Johnston, comb. nov. [based on: *Potentilla modesta* Rydb. N. Amer. Fl. 22: 331. 1908]. Sagebrush, meadow, aspen, spruce-fir, and Douglas fir communities at 2280 to 3480 m in Carbon, Emery, Garfield, Piute (type from Mt. Barrett near Marysvale), Sanpete, Sevier, Wasatch, and Wayne counties, endemic. The *modesta* phase of the pretty cinquefoil occurs generally above the range of var. *bicrenata*, with which it forms occasional intermediates. Specimens from Emery and Sanpete counties approach var. *divisa* Rydb. and *P. gracilis*; 18 (iii).

Var. *proxima* (Rydb.) Welsh & Johnston comb. nov. [based on *Potentilla proxima* Rydb. N. Amer. Fl. 22(4): 339. 1908. (*P. beanii* Clokey; "*P. quinquefolia*" sens. Rydb.)]. Pinyon-juniper, sagebrush, ponderosa pine, and spruce-fir communities at 2200 to 3000 m in Carbon, Garfield, Iron, Piute, and Wayne counties; Nevada; 34 (iii).

Potentilla crinita **Gray** Hair-tuft Cinquefoil. Perennial herbs, the stems ascending to erect, 1.3–4.3 dm tall; leaves mainly basal, pinnately 7- to 13-foliolate, the terminal leaflet 0.6–3 cm long, 0.2–0.9 cm wide, elliptic-oblong to narrowly oblanceolate, toothed at the apex only (somewhat below on some leaves), not markedly bicolored, pilose and sometimes slightly tomentose beneath, strigose-pilose to glabrate above; cauline leaves 2 or 3; cymes several to many flowered, the flowers showy; sepals 3–5.4 mm long, oblong-lanceolate, acuminate; petals yellow, 5–6.5 mm long; achenes several, 1.3–1.8 mm long; styles subapical, filiform, 1.8–2.1 mm long. Two moderately distinctive varieties are represented:

1. Leaflets 11–15, uniformly long-strigose, not bicolored, with 5–19 teeth, often small, curled, and folded, without tomentum .... *P. crinita* var. *crinita*

— Leaflets 7–12, long-strigose below, tomentose above, somewhat bicolored, with 5–11 teeth, sometimes larger and flat; tomentose on stems, leaves, and petioles .... *P. crinita* var. *lemmonii*

Var. *crinita*. (*P. vallicola* Greene). Sagebrush, mountain brush, pinyon-juniper, ponderosa pine, and aspen communities at 1890 to 2200 m in Wayne and Garfield counties; Arizona, New Mexico, and Colorado. The varieties are connected by intermediates; 10 (iii).

Var. *lemmonii* (Wats.) Kearney & Peebles [*P. lemmonii* (Wats.) Greene; *Ivesia lemmonii* Wats.]. Mountain brush, pinyon-juniper, ponderosa pine, and aspen communities at 1900 to 2590 m in Garfield, Iron, Kane, Piute, and Wayne counties; Arizona, Nevada, and New Mexico. This variety is intermediate between var. *crinita* and *P. hippiana*, but is distinguished from *P. hippiana* by the narrow, few-toothed leaflets, strigose-glandular pubescence, and openly branched inflorescence with smaller flowers. To these *crinita* characteristics are combined the *hippiana* character of tomentum and bicolored leaves. Some few specimens are apparently exactly intermediate between var. *lemmonii* and *P. hippiana*, and possibly represent products of hybridization; 20 (v).

Potentilla diversifolia **Lehm.** Wedge-leaf Cinquefoil. Perennial herbs, the stems ascending to erect, 0.6–3.2 dm tall; leaves mainly basal, palmately to less commonly pinnately (3) 5- to 7-foliolate, the terminal leaflet 1.2–4 cm long, 0.3–1.8 cm wide, obovate to oblanceolate, toothed mainly above the middle, not bicolored, green on both sides, strigose to pilose on both sides, seldom tomentose below; cauline leaves 1–3; cymes several flowered, the flowers showy; sepals 5–6.5 mm long, triangular to triangular-attenuate; bracteoles 2.1–4.5 mm long, oblong to lanceolate; petals yellow, 5.6–9.5 mm long; achenes numerous, 1.5–1.9 mm long; style subapical, 1.9–2.6 mm long, smooth or glandular, not basally thickened. Two varieties are present:

1. Leaflets divided 70–90 percent to midrib, into narrowly oblong segments; plants 15–20 cm tall, of the Uinta Mts. .... *P. diversifolia* var. *perdissecta*
— Leaflets divided 40–70 percent to midrib, or usually merely toothed; plants 15–30 cm tall, widespread in mountains .... *P. diversifolia* var. *diversifolia*

Var. *diversifolia.* (*P. glaucophylla* Lehm.; *P. concinniformis* Rydb.). Dry to wet meadows, lake margins, stream banks, forest margins, alpine tundra, and rocky ridges at 2745 to 3500 m in Beaver, Cache, Daggett, Duchesne, Garfield, Grand, Iron, Juab, Piute, Salt Lake, San Juan, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, Washington, and Wayne counties; Alaska and Yukon, south to California, Arizona, New Mexico, and South Dakota. This is a highly variable taxon. The following variety is the most pronounced of regional ecotypes, but is weak and difficult to distinguish in all cases; 50 (xv).

Var. ***perdissecta*** **(Rydb.) C. L. Hitchc.** (*P. perdissecta* Rydb.). Rare in Utah, at 3100 m in the Uinta Mts., Summit Co.; Wyoming, Idaho, and Montana, and less commonly north in Canada; 38 (0).

Potentilla effusa **Dougl. ex Lehm.** (*P. coloradensis* Rydb.) Perennial herbs, multicipital from a branched caudex; stems ascending to erect, 2–4 dm tall; basal leaves 3.5–13 cm long, pinnately compound with 5–11 leaflets, the terminal one 2.0–4.0 cm long, 0.5–1 cm wide, oblanceolate to obovate, serrate or toothed about one half of way to midrib, the teeth only above the middle of the leaflet, sometimes apically few-toothed, white or grayish-tomentose above and below, never strongly bicolored; flowers several to many; sepals 3.5–4.7 mm long, lance-ovate, acuminate, conspicuously tomentose especially at anthesis; bracteoles 1.0–2.8 mm long, usually shorter than the calyx-lobes and darker in color; petals yellow, 4.0–6.5 mm long; achenes numerous; styles subapical, 1.9–2.8 mm long, filiform. Rare, rocky slopes and shelves of cliffs, north slope of the Uinta Mts. at 2740 m, Summit and Daggett counties; Colorado to central Alberta, almost always on the eastern slope of the Continental Divide; 3 (i).

Potentilla fissa **Nutt.** (*Drymocallis fissa* (Nutt.) Rydb.) Perennial glandular-pubescent herbs, low, 2–3 dm tall, from a caudex; basal leaves conspicuously veiny, dark green, pinnately compound with 7–13 leaflets, the terminal one 1–5 cm long and 1–3 cm wide, broadly ovate to orbicular, deeply incised and doubly serrate, glandular-puberulent to glabrous on both surfaces; flowers several to many; sepals 5–10 mm long, long-acuminate, longer in fruit; bracteoles 4–6 mm long, narrowly lanceolate; petals yellow, orbicular, concave, 6–9 mm long; styles basally attached, 0.8–1.0 mm long, deltoid. Reported from Utah by Rydberg (1908, 1922); one specimen from Utah Co. at 2070 m.; southwestern Colorado, southwestern Wyoming and central Idaho, north to Alberta and South Dakota, south to New Mexico.

Potentilla fruticosa **L.** Shrubby Cinquefoil; Yellow Rose; Tundra Rose. [*Fragaria fruticosa* (L.) Crantz; *Dasiphora riparia* Raf.; *D. fruticosa* (L.) Rydb.; *P. floribunda* Pursh; *Pentaphylloides floribunda* (Pursh) A. Love]. Shrubs to 1 m tall or more; bark shreddy; leaves 1–5 cm long, pinnately 3- to 7-foliolate, the terminal leaflet 0.5–2.5 cm long, 0.2–1 cm broad, oblong to elliptic, entire, green and sparsely hairy to glabrate above, grayish and silvery hairy below, somewhat revolute; flowers 1 to several, conspicuous; sepals 3.5–9 mm long, ovate-lanceolate; bracteoles 4–13 mm long, lanceolate to elliptic; petals yellow, 6–14 mm long, rounded; receptacle hairy; achenes 1.5–2 mm long, white-hairy. Meadows, sagebrush, aspen, lodgepole, ponderosa pine, and spruce-fir communities often on floodplains or stream banks at 1700 to 3500 m in Carbon, Daggett, Duchesne, Garfield, Grand, Iron, Kane, Piute, San Juan, Salt Lake, Sanpete, Sevier, Summit, Uintah, Utah, Wasatch, and Wayne counties; Alaska east to Newfoundland, south to California, New Mexico, Iowa, and New Jersey; Eurasia. This handsome plant is known in cultivation in Utah, Summit, and Salt Lake counties at elevations below 1900 m, and should be grown widely in the state; 62 (ix).

Potentilla glandulosa **Lindl.** Glandular Cinquefoil. [*Drymocallis glandulosa* (Lindl.) Rydb.] Perennial glandular-pubescent herbs, 0.8–6 (7) dm tall, from a caudex; basal leaves 3–22 cm long, pinnately compound, with 5–9 leaflets, the terminal one 0.7–6.8 cm long, 0.6–4.2 cm wide, obovate to elliptic, doubly dentate or lobed, green and variously pubescent or glandular on both surfaces; flowers several to many, showy or inconspicuous; sepals 5.5–9.3 mm long, lance-ovate, often acuminate, longer in fruit; bracteoles 4.5–7.2 mm long, oblong to narrowly lanceolate; petals mainly yellow, mostly 4–7.5 mm long; receptacle sparsely hairy; achenes numerous, 1–1.2 mm long; styles from below the middle, 0.8–1 mm long. The glandular cinquefoil is widespread and common in much of Utah, where it consists of a series of intergrading populations varying by degree from each other and only arbitrarily separable from *P. arguta* (q.v.), with which it probably should be combined. In that case, the name would be *P. arguta*, because that epithet has priority. The complex was summarized by Keck (Carnegie Institution Washington 520: 26–124. 1940). He recognized four morphological phases from Utah (i.e., the subspecies *arizonica*, *micropetala*, *glabrata*, and *pseudorupestris*). Examination of a fairly large series of specimens from Utah demonstrates that all, except that designated as *micropetala* are connected by a series of intermediates, and might best be regarded as belonging to a single polymorphic and highly plastic var. *intermedia*. The following key will serve to differentiate most specimens.

1. Petals much shorter than the sepals, 4–5 mm long, 2–4 mm broad .... *P. glandulosa* var. *micropetala*

— Petals shorter than to slightly exceeding the sepals, mainly 5–7.5 mm long and about as broad .... *P. glandulosa* var. *intermedia*

Var. *intermedia* (Rydb.) C. L. Hitchc. [*Drymocallis pseudorupestris* var. *intermedia* Rydb.; *D. glabrata* Rydb.; *P. glandulosa* ssp. *glabrata* (Rydb.) Keck; *P. glandulosa* var. *glutinosa* f. *glabrata* (Rydb.) T. Wolf; *D. arizonica* Rydb.; *P. glandulosa* ssp. *arizonica* (Rydb.) Keck; *P. macdougalii* Tidestr.; *P. pseudorupestris* Rydb.; *D. pseudorupestris* (Rydb.) Keck]. Mountain brush, ponderosa pine, lodgepole pine, aspen, and spruce-fir communities, often in meadows at 1890 to 3200 m in Beaver, Box Elder, Cache, Daggett, Duchesne, Garfield, Piute, Rich, Salt Lake, Sanpete, Sevier, Summit, Uintah, Utah, Wasatch, Washington, and Weber counties; British Columbia and Alberta south to Oregon, Arizona, and Wyoming; 33 (iv).

Var. *micropetala* (Rydb.) Welsh & Johnston, comb. nov. [based on: *Drymocallis micropetala* Rydberg, North Amer. Flora 22(4): 375. 1908. Type from Salt Lake Co.; *P. glandulosa* ssp. *micropetala* (Rydb.) Keck]. Sagebrush, mountain brush, upwards to alpine meadows at 1430 to 3050 m in Salt Lake, Sanpete, Sevier, and Weber counties; Idaho and Wyoming. This small-petaled phase resembles *P. norvegica* in flower size and in general conformation, but differs from inter alia in pistil features and leaflet number; 4 (i).

Potentilla gracilis **Dougl. ex Hook.** Slender Cinquefoil. Perennial, variably pubescent herbs from a caudex; stems ascending to erect, 0.4–6 (8) dm tall; basal leaves 3–30 cm long, or more, palmately compound, with 5–9 leaflets, the terminal one 1.3–10.7 cm long, 0.4–3.7 cm wide, obovate to oblanceolate, crenate, serrate, or toothed to dissected, commonly slightly bicolored, green on both sides; flowers several to numerous, showy; sepals 3.5–9.5 mm long, lanceolate to lance-ovate, acute to attenuate-acuminate; bracteoles 2.4–8.5 mm long, lance-oblong; petals yellow, 5.6–8 (10) mm long; achenes numerous, 1.3–1.6 mm long; styles subapical, 2–2.3 mm long, filiform or thickened to about half the length, tapered to stigma. Several intergrading phases are recognizable at varietal level in this most common and widespread of our cinquefoil species. Variants tend to represent recombinant types of several recurrent features: glands on calyx teeth, tomentum on lower leaflet surface, and depth of incision of leaflet margin. There are two varieties separable as follows:

1. Calyx lobes and often the leaflets glandular and stiffly pilose; plants often drying brownish .... *P. gracilis* var. *brunnescens*

— Calyx lobes and leaflets without glandular hairs; plants usually green .... *P. gracilis* var. *glabrata*

Var. ***brunnescens*** **(Rydb.) C. L. Hitchc.** (*P. brunnescens* Rydb.). Meadows, mountain brush, aspen, spruce-fir, and alpine tundra at 2300 to 3180 m in Salt Lake, Sanpete, Sevier, Summit, and Utah counties; Washington and Montana south to Nevada and Wyoming. This variety is freely transitional to *P. pulcherrima* and to *P. diversifolia*, where they occur together; 9 (0).

Var. ***glabrata*** **(Lehm.) C. L. Hitchc.** [*P. nuttallii* var. *glabrata* Lehm.; *P. glabrata* (Lehm.) Rydb.; *P. chrysantha* Lehm. in Hook., not Trev.; *P. gracilis* var. *chrysantha* (Lehm.) Rydb.; *P. rigida* Nutt.; *P. gracilis* var. *rigida* (Nutt.) Wats.; *P. gracilis* var. *nuttallii* Sheld.; *P. gracilis* ssp. *nuttallii* (Sheld.) Keck; *P. blaschkeana* Turcz. ex Lehm.; *P. gracilis* var. *blaschkeana* (Turcz.) Jeps.; *P. viridescens* Rydb.; *P. gracilis* var. *viridescens* (Rydb.) T. Wolf; *P. glomerata* A. Nels.; *P. blaschkeana* var. *glomerata* (A. Nels.) T. Wolf; *P. jucunda* A. Nels.; *P. diversifolia* var. *jucunda* (A. Nels.) T. Wolf; *P. grosseserrata* Rydb.; *P. rectiformis* Rydb.; *P. dichroa* Rydb.; *P. permollis* Rydb.; *P. gracilis* var. *permollis* (Rydb.) C. L. Hitchc.]. Mountain brush, sagebrush, aspen, and spruce-fir communities at 1675 to 2745 m in Daggett, Piute, Sanpete, Sevier, and Weber counties; British Columbia and Alberta south to California, New Mexico, and Nebraska. Included in our limited materials are those specimens with spreading hairs on petioles and stems, passing as var. *permollis* (Rydb.) C. L. Hitchc. They seem to be transitional completely with var. *glabrata*; 7 (i).

Potentilla hippiana **Lehm.** Hipp Cinquefoil; Woolly Cinquefoil. [*P. leucophylla* Torr., not Pallas; *P. pensylvanica* var. *hippiana* (Lehm.) T. & G.; *Pentaphyllum hippianum* (Lehm.) Lunnell; *P. effusa* var. *filicaulis* Nutt. in T. & G.; *P. filicaulis* (Nutt.) Rydb.; *P. diffusa* Gray; *P. hippiana* var. *diffusa* (Gray) Lehm.; *P. hippiana* var. *propinqua* Rydb.; *P. propinqua* (Rydb.) Rydb.; *P. argyrea* Rydb.; *P. hippiana* var. *argyrea* (Rydb.) B. Boi.]. Perennial, variably pubescent herbs from a caudex, the stems ascending to erect, 1.1–4.8 (5.5) dm tall; basal leaves 2.5–19 cm long or more, pinnately compound with 7–11 leaflets, the terminal one 0.9–4.7 cm long, 0.4–1.9 cm wide, oblanceolate to oblong or elliptic, serrate or toothed less than halfway to midrib, the teeth from below the middle, grayish-tomentose to pilose on one or both surfaces; flowers several to numerous, showy; sepals 4.3–6.5 mm long, lance-ovate, acute to acuminate; bracteoles 2.4–5.5 mm long, lance-oblong; petals yellow, 6–7.7 (9.5) mm long; achenes several to numerous, 1.5–1.9 mm long; styles subapical, 1.8–2.3 mm long. Meadow, aspen, spruce-fir, and alpine tundra communities at 2250 to 3450 m in Beaver, Daggett, Duchesne, Garfield, Grand, Iron, Piute, San Juan, Sevier, Summit, Uintah (?), Washington, and Wayne counties; British Columbia east to Michigan and south to New Mexico, Arizona, and Nebraska. Apparent intermediates are known between the Hipp cinquefoil and *P. gracilis*, and especially *P. pulcherrima*; 18 (1).

Potentilla hookeriana **Lehm.** Hooker Cinquefoil. Perennial herbs, the stems ascending, 1–2 dm tall, from a caudex; leaves 1–3 cm long, all basal, ternate-digitate, the terminal leaflet 1–3 cm long, 0.5–1.5 cm wide, ovate to obovate, shallowly few toothed, densely white-tomentose below and sparsely tomentose to puberulent above, bicolored; petiole sericeous-strigose and tomentose; flowers 3–15, small; sepals 4–8 mm long, lanceolate-acuminate; bracteoles 3–6 mm long, lanceolate-acuminate, densely villous and tomentose; petals yellow, obcordate, 2–5 mm long; achenes numerous; style subterminal, 0.8–1 mm long, usually uniformly thickened. Alpine grassland and tundra, 3350 to 3360 m in Summit, Duchesne, Grand, and Juab counties; Greenland to Alaska and south to Wyoming and Colorado; 4 (ii).

Potentilla multisecta **(Wats.) Rydb.** Dissected Cinquefoil. [*P. diversifolia* var. *multisecta* Wats.]. Perennial herbs; stems decumbent to ascending, 1–1.5 dm long, from a caudex; leaves (4) 5–8 (9) cm long, mainly basal, palmate to subpinnate, with 5–8 (12) leaflets, the terminal leaflet 1–4 cm long, and 1–2 cm wide, ovate to obovate, pinnately dissected into 3–8 long narrow segments, deeply divided, moderately to densely strigose, often grayish green; flowers 3–10, on recurved pedicels in fruit; sepals 3–6 mm long, strigose to strigulose; bracteoles 2–4 mm long, lanceolate-acuminate, strigose to strigulose; petals yellow, obcordate, 4–8 mm long; style subterminal, 2–1.3 mm long, filiform. Pinyon-juniper and sagebrush communities, rocky ridges of foothills at 2075 to 3000 m in Juab and Tooele counties; Nevada. Plants of open places are low, with the leaf rachis short, but shade forms and those from rock crevices and ledges are large and lax. This entity had often been compared with *P. diversifolia* var. *perdissecta*, but is distinctive in its strigose pubescence and recurved pedicels, and its habitat is at much lower elevations in drier sites. In habit, the plants resemble *P. concinna*, especially its var. *proxima*, but differ in the much more dissected leaflets, absence of tomentum, and recurved pedicels; 20 (iii).

Potentilla nivea **L.** Perennial nonglandular herb, the stem decumbent to ascending, 0.7–2 dm long, from a caudex; stems and petioles densely tomentose; basal leaves 2–9 cm long, trifoliolate, the terminal leaflet 0.8–2.7 cm long, 0.7–1.7 cm wide, obovate to elliptic or oblanceolate, coarsely toothed to near the base, green and silky-pubescent above, densely snow white tomentose below, strongly bicolored; flowers 1–15 in an open inflorescence, showy; sepals 2.5–5 mm long, lanceolate; bracteoles 1.8–4.5 mm long, oblong to lanceolate; petals yellow, 4–7 mm long; achenes several, 1–1.5 mm long; style subterminal, ca 1 mm long, uniformly thickened. Alpine tundra in the LaSal Mts., Grand and San Juan counties; Alaska east to Greenland, south in the Rocky Mountains to New Mexico and southeastern Utah; Eurasia; 8 (iii). This species is common and distinctive through the Rocky Mts., and probably should be expected in the Uinta Mts. as well.

Potentilla norvegica **L.** Rough Cinquefoil. [*Fragaria norvegica* (L.) Crantz; *P. monspeliensis* var. *norvegica* (L.) Farw.; *P. monspeliensis* L.; *Fragaria monspeliensis* (L.) Crantz; *P. norvegica* ssp. *monspeliensis* (L.) Asch. & Graebn.; *P. hirsuta* (Michx.) Hylander]. Annual or biennial (short-lived perennial?) herbs, the stems erect, 0.7–5 dm tall or more, from a taproot, the stems and petioles sparsely stiff-hairy; leaves mostly cauline, palmately (or subpinnately) compound with 3 (rarely 5) leaflets, the terminal one 1–8 cm long, 0.6–2.7 cm wide, obovate to oblanceolate, coarsely toothed to near the base or entire and cuneate in the lower part, green and sparsely stiff-hairy to glabrous above, paler and stiff-hairy beneath, especially along the veins; flowers several to many, inconspicuous; sepals 4–6 mm long, ovate-lanceolate, enlarging in fruit; bracteoles 3–6 mm long, oblong to elliptic or lanceolate; petals yellow or whitish, 2.5–3.6 mm long; achenes numerous, 0.8–1.1 mm long; style subterminal, 1.6–0.9 mm long. Floodplains, wet meadows, lake shores and other moist sites at 1370 to 2930 m in Garfield, Grand, Iron, Kane, Salt Lake, Sevier, Uintah, and Utah counties; widely distributed in the northern hemisphere; 8 (i).

Potentilla ovina **Macoun** Perennial herbs, from a caudex, the stems decumbent to ascending, 1–3.5 (5) dm tall; leaves mainly basal, pinnately compound with (5) 9–18 leaflets, the terminal mostly 0.6–2.1 mm long, 0.4–1.1 cm wide, deeply pinnately dissected or apically few toothed, conspicuous; calyx 6–8 (10) mm long, lobes ovate-lanceolate to lance-attenuate; bracteoles 1.8–4 mm long, oblong to lance-oblong; petals yellow, 5–6.4 mm long; achenes many, 1.1–1.7 mm long; style subterminal, 1.8–2.7 mm long, filiform. There are two fairly distinct varieties in Utah:

1 Leaflets densely to uniformly sericeous, grayish green or gray, often with a lower layer of sparse tomentum, 5–10 mm long, often with more than 6 teeth; leaf rachis 2–6 cm long .... *P. ovina* var. *ovina*

— Leaflets glabrous to sparsely sericeous-strigose, usually green, never tomentose, 10–20 mm long, often with 3–5 teeth; leaf rachis 3–12 cm long .... *P. ovina* var. *decurrens*

Var. *decurrens* **(Wat.) Welsh & Johnston,** comb. nov. [based on: *Potentilla dissecta* var. *decurrens* Wats., Proc. Amer. Acad. 8: 557, 565. 1873; *P. nelsoniana* Rydb.]. Meadows and rocky ridges, ponderosa pine, lodgepole, spruce-fir, aspen, and (less commonly) alpine tundra communities at 2200–3500 m in Beaver, Cache, Daggett, Duchesne, Garfield, Grand, Piute, San Juan, Sanpete, Summit, Tooele, Uintah, and Wayne counties; southern Colorado west to central Nevada, north to southern Wyoming, more sparsely northward to Alberta. This is a characteristic form of montane meadows in the Uinta Mts., up to the alpine there and elsewhere.

Var. *ovina* [*P. diversifolia* var. *pinnatisecta* Wats.; *P. wyomingensis* A. Nels.; *P. monidensis* A. Nels.]. Meadows and rocky ridges, openings in spruce-fir and alpine tundra communities, 2800–3900 m in Cache, Davis, Duchesne, Grand, Juab, Piute, Salt Lake, San Juan, Sanpete, Utah, and Summit counties; southwestern Alberta south to northeastern Oregon, central Utah, and southern Wyoming. This taxon has been confused with *P. plattensis*, but its tomentulose leaflets and erect-ascending pedicels in fruit appear to be diagnostic. Hybrids between *P. ovina* (usually var. *decurrens*) and *P. pulcherrima* are frequently encountered in Utah (Box Elder, Cache, Piute, Daggett, and Summit counties); leaves are pinnate or subpalmate with 7–15 leaflets that are usually bicolored and moderately tomentose beneath, and stems are ascending, contrasting with the usually decumbent *ovina* and the erect-ascending *pulcherrima*.

Potentilla paradoxa **Nutt. in T. & G.** Contrary Cinquefoil. [*P. supina* Michx., not L.; *Tridophyllum paradoxum* (Michx.) Greene; *P. supina* var. *nicolletii* Wats.] Annual, biennial or short-lived perennial herbs, the stems decumbent to ascending or erect, 0.8–9 dm tall, sparsely to moderately villous; leaves mainly cauline, all pinnately compound with 5–11 leaflets, the terminal one 1.2–4.5 cm long, 0.4–2.5 cm wide, often dissected into 3 main confluent lobes, obovate to oblanceolate, toothed to below the middle, cuneate to the base, green on both sides, strigose to strigulose; flowers few to many, not especially showy; sepals 3–5.2 mm long, ovate, shorter than the bracteoles, enlarging in fruit; bracteoles 4–6.5 mm long, lanceolate; petals yellow or whitish, 3.2–4.3 mm long; achenes numerous, 0.8–1 mm long, laterally enlarged along ventral suture; style subterminal, 0.5–0.7 mm long. Beaches, marshes, and lake shores at 1350 to 1650 m in Salt Lake and Utah counties; widespread in North America; Asia; 6 (0).

Potentilla pectinisecta **Rydb.** [*P. candida* Rydb.; *P. pecten* Rydb.] Perennial herbs, 3–4 dm tall; stems stout and erect to ascending from a caudex, silky-strigose; leaves mostly basal, strictly palmate with 5–9 leaflets, the leaflets oblanceolate, silky-strigose on both sides, sometimes also sparsely tomentose beneath, deeply pectinately divided in oblong-linear segments; inflorescence glomerately many-flowered with relatively thick pedicels; flowers large and showy; calyx silky-sericeous, 6–9 mm long, with lanceolate-acuminate lobes; petals yellow, obcordate-emarginate, 7⅓ mm long; styles uniformly thickened about one-half the length then filiform above, 1.8–3.2 mm long. Rare, at 2150 to 2750 m in Tooele and Salt Lake counties; Wyoming (?).

Potentilla pensylvanica **L.** Perennial, glandular to nonglandular herbs from a caudex, the stems ascending to erect, 0.5–4.5 dm tall or more; leaves mostly basal, 2–18 (25) cm long, erect, pinnately compound with 5–17 leaflets, the terminal one 0.9–4.5 (6) cm long and 0.4–1.2 cm wide, elliptic to oblong or oblanceolate, coarsely toothed to narrowly lobed, the sinuses extending more than half way to the midrib, conspicuously revolute margined, green and somewhat hairy above, white or more commonly greenish or yellowish tomentose below; flowers few to many in a glomerate inflorescence, showy; sepals 3.5–7.5 mm long, ovate-lanceolate; bracteoles 3–6 mm long, narrowly lanceolate; petals yellow, 5–8 mm long; receptacle glabrous; achenes numerous, 0.9–1.2 mm long; style subterminal, 0.9–1.0 mm long, coniform, with a conspicuously thickened and often pappillose base. This is a highly variable species throughout its large range in North America; the taxonomic problems in this species are mirrored in the whole section (sect. Multifidae), to which *P. rubricaulis* and *P. multifida* belong. These are misunderstood and complex species of the western and eastern hemispheres, respectively. There is seemingly only one entity in Utah that merits separation from typical *P. pensylvanica*:

1. Leaflets 5–7, subdigitate (10–30 percent of the rachis occupied with leaflets); pubescence silvery or yellowish white, often of long entangled hairs densely matted; plants alpine, La Sal and Tushar Mts. .... *P. pensylvanica* var. *paucijuga*

– Leaflets 7–17, often pinnate (30–60 percent of rachis occupied); pubescence olive greenish, dull, not silvery, usually composed of short curly hairs sparsely matted; plants widespread, rarely alpine in Uinta Mts. .... *P. pensylvanica* var. *pensylvanica*

Var. ***paucijuga*** **(Rydb.) Welsh & Johnston,** comb. nov. [based on: *Potentilla paucijuga* Rydb. N. Amer. Fl 22(4): 348. 1908. Type from La Sal Mts., *Purpus* 251 in August 1899 (US! photo NY!)]. Grassy tundra, alpine communities, at 3800 m in Grand, Piute, and San Juan counties; endemic to Utah. In the LaSal Mts. this form may hybridize with *P. nivea*; the two species are usually distinguished by the glomerate inflorescence with glandular pubescence, revolute-margined leaflets, and pinnate leaves of var. *paucijuga*. Another variety of this species occurs in similar situations in California (var. *ovium* Jeps., not *P. pseudosericea* Rydb.), and it is possible that other alpine ecotypes of *P. pensylvanica* deserve recognition in the Great Basin; 11 (ii).

Var. ***pensylvanica*** [*P. pseudosericea* Rydb.; *P. arachnoidea* (Lehm.) Dougl. ex Rydb.] Sagebrush, sagebrush-grass, and meadow communities at 2200–3450 m in Beaver, Carbon, Duchesne, Emery, Garfield, Grand, Iron, Sevier, Wayne, and Wasatch counties; Hudson Bay to Alaska, south to northern Mexico, Texas, and Arizona. 38 (v).

Potentilla plattensis **Nutt.** [*Ivesia pinnatifida* Wats.; *P. arizonica* Greene; *P. plattensis* var. *pedicellata* A. Nels.]. Perennial herbs with stems 0.5–2.5 dm long, decumbent or creeping through meadow herbs and grasses; leaves basal and cauline, 3–11 cm long, pinnately compound with 11–23 leaflets, these verticillate or subverticillate; terminal and lower leaflets all pinnately toothed with 5–8 teeth cutting 70–90 percent to midrib, glabrous to sparsely strigose, green to grayish green on both surfaces; stems with 3–15 flowers on recurved pedicels in fruit; calyx (5) 6–8 mm long, strigose or puberulent; achenes numerous; styles subterminal, 1.5–3.0 mm long, filiform. Wet meadows, bogs, and valley bottoms, rare in Utah, 1820–2700 m in Cache, Kane, and Sevier counties; Alberta and Manitoba south through Wyoming and

Colorado to central Arizona and New Mexico. This species has been confused with *P. ovina* in the past, but the habitats are usually sharply distinct, and the combination of trailing stems, pinnately dissected leaflets, subglabrous pubescence, and recurved pedicels are diagnostic for *P. plattensis.* Sometimes there are two forms at the same site: a lax trailing form in moist portions of a meadow, and a more compact form with prostrate stems on better-drained soil in the same meadow.

Potentilla pulcherrima **Lehm.** [*P. filipes* Rydb.; *P. wardii* Greene; type from Thousand Lake Mtn., Wayne Co.]. Perennial herbs, 3–8 dm tall, erect to ascending from a caudex; leaves mostly basal on long petioles, 8–25 cm long, palmate or subpinnate with 7 (9) leaflets, the terminal leaflet 1.5–8 cm long and 1–3.5 cm wide, oblanceolate or spatulate, with 10–15 coarse teeth cutting less than one-half, sericeous or strigose above, densely tomentose below, strongly bicolored; stem with 10–40 flowers that are large and showy; calyx large, 8–12 mm high, with acuminate lobes, sericeous-strigose and sometimes glandular in addition; petals yellow, 7–14 mm long; style filiform or slightly thickened at base, 1.6–3.0 mm long. Meadows and rocky slopes, pinyon-juniper, ponderosa pine, mountain shrub, and aspen communities at 2200 to 3380 m in Beaver, Box Elder, Carbon, Daggett, Garfield, Grand, Iron, Piute, San Juan, Duchesne, Emery, Salt Lake, Sanpete, Sevier, Summit, Uintah, Utah, Wasatch, and Wayne counties; British Columbia east to Quebec, south to New Mexico, Arizona, and Nevada; 66 (xiii). This species has often been compared with *P. gracilis*, but seems distinctive in its bicolored leaves, style form, oblanceolate leaflets, glandular pubescence, and longer petioles. It has also been confused with *P. concinna*, but contrasts with the strigose pubescence, prostrate habit, few-flowered inflorescence, and the simply acute calyx lobes and bracteoles of that species. Hybrid swarms are fairly frequent between *P. pulcherrima* and *P. hippiana* (Garfield, Grand, Piute, San Juan, Sevier, Summit, and Wayne counties), in which any combination of the distinguishing characters may be found.

Potentilla rivalis **Nutt.** [*P. millegrana* Engelm. ex Lehm; *P. leucocarpa* Rydb. in Britt. & Br.] Annual or biennial herbs from a taproot, the stems 2–6 dm tall, spreading to suberect, pubescent with fine villous or villous-tomentose hairs; leaves mainly cauline, palmately to subpinnately compound with 3–5 leaflets, the terminal 1–4 cm long, 0.4–1.3 cm wide, obovate to oblong to oblanceolate, coarsely toothed (at least above the middle), green and minutely villous on both sides; flowers numerous, inconspicuous; sepals 2.3–4.2 mm long, ovate; bracteoles 3.3–4 mm long, lanceolate; petals yellow, 1.5–1.9 mm long, not enlarged laterally; style subterminal, 0.6–0.8 mm long, fusiform. Reservoir shore at 2300 m in Carbon Co., and to be expected elsewhere; widespread in North America; 1 (i).

Potentilla rubricaulis **Lehm.** [*P. saximontana* Rydb; *P. pedersenii* Rydb.; *P. furcata* Porsild]. Perennial herbs, stems ascending from a caudex, leaves mostly basal, eglandular, palmate to subpinnate with 5–7 leaflets, the terminal one 1.0–2.5 cm long and 0.5–1.0 cm wide, few toothed with narrow-crenate or serrate teeth, usually deeply divided 50–90 percent, often revolute margined, densely grayish-tomentose below, sparsely tomentose to puberulent above, strongly bicolored, often pilose as well below with tufts of hair at the tips of ultimate segments, the petioles pilose-sericeous with subsidiary tomentum; cymes 1- to 10-flowered, the flowers showy but small; sepals 4–6 mm long; bracteoles 3–6 mm long; style subapical, 0.9–1.1 mm long, conic, usually conspicuously thickened and papillose below. Alpine tundra meadows and rocky ridges, 3600 to 4000 m in Duchesne, Grand, Piute, San Juan, and Summit counties; Greenland to Alaska, south to British Columbia, sparsely and rarely through Montana into Wyoming, and Colorado. This name is very often misapplied, but here it is taken for a strictly alpine species with cone-shaped, thickened style about one mm long, more or less digitate leaves with 5–7 leaflets, and petioles with long straight hair in addition to tomentum. It has affinities with sect. Multijugae (see *P. pensylvanica*), but may be related to *P. nivea* and its relatives as well, with which it may hybridize; 5 (0).

Prunus L.

Shrubs or small trees with unarmed branches; leaves alternate, simple, entire to serrate or serrulate, rarely lobed, commonly with glands on petioles or blade bases; stipules lance-attenuate to linear, caducous; flowers perfect, regular, solitary, in umbellate clusters, or in racemes; sepals 5, borne atop a cup-shaped to turbinate hypanthium; petals 5, white, pink, rose, or red; stamens numerous; pistil 1, free from the usually deciduous hypanthium; style 1, elongate, with capitate stigma; fruit a drupe. **Note:** The genus is represented by only two indigenous species in Utah, *P. fasciculata* and *P. virginiana*. However, the numerous cultivated species persist following cultivation, and many escape. They are treated herein for those reasons.

1. Leaves entire or serrate only near the apex, borne in fascicles, less than 2 cm long and 0.5 cm wide; shrubs with divaricate branches, of low elevations, indigenous in Millard, Beaver, and Washington counties .... *P. fasciculata*
— Leaves various, usually larger; shrubs to trees of moderate size, variously distributed, but not of desert shrublands 2

2(1). Flowers borne in pedunculate, elongate, or corymbose clusters 3
— Flowers borne singly or in sessile umbellate clusters from winter buds 7

3(2). Flowers borne in corymbose racemes, the pedicels subtended by persistent bracts 4
— Flowers borne in elongate racemes, the pedicels without persistent bracts 5

4(3). Flowers to 2 cm wide or more, the petals often pink or double or both; bracts 3–8 mm long, cuneate, the truncate apex fringed-serrulate; flowering cherry .... *P. serrulata*
— Flowers ca 0.8 cm wide, the petals white, single; bracts ca 1 mm long, ovate, serrulate; escaping (rootstock) .... *P. mahaleb*

5(3). Leaves leathery, thickened, more or less evergreen, entire; plants cultivated shrubs .... *P. laurocerasus*
— Leaves not especially thickened, serrate to serrulate; shrubs or small trees, cultivated or not 6

6(5). Hypanthium pubescent within; racemes pendulous or spreading in anthesis; cultivated ornamental .... *P. padus*
— Hypanthium glabrous within; racemes erect or ascending in anthesis; indigenous or less commonly cultivated .... *P. virginiana*

7(2). Leaves cordate-ovate to broadly ovate; cultivated apricot, rarely escaping .... *P. armeniaca*
— Leaves lanceolate to oblong, or less commonly oblanceolate to broadly elliptic; cultivated ornamental and fruit trees and shrubs 8

8(7). Plants shrublike, mainly 2 m tall or lower 9
— Plants shrub- or treelike, mainly 2–5 m tall or more 11

9(8). Leaves glabrous, less than 2 cm broad; flowers commonly 2–4 per bud .... *P. besseyi*
— Leaves hairy,at least along veins beneath; flowers solitary (rarely 2) per bud 10

10(9). Leaves long-villous beneath, sparingly villosulose above, broadly elliptic to oblong; flowers single; cultivated for ornament and for fruit .... *P. tomentosa*
— Leaves sparingly villous on both sides; flowers mostly double; cultivated ornamental .... *P. triloba*

11(8). Flowers solitary, or sometimes 2 or 3 per bud 12

— Flowers 3 or more per bud 15

12(11). Axillary buds on fruiting branchlets borne in 3s, the lateral ones producing flowers 13

— Axillary buds on fruiting branchlets borne singly 14

13(12). Leaves pubescent beneath; pedicels pubescent; cultivated plum .... *P. domestica*

— Leaves glabrous beneath, except on midrib; pedicels glabrous; cultivated flowering plum .... *P. ceracifera*

14(12). Leaves sharply serrate; fruit not leathery and splitting, exposing the stone at maturity; cultivated peach, commonly escaping .... *P. persica*

— Leaves crenate-serrate; fruit leathery, splitting and exposing stone at maturity; sparingly cultivated almond, not escaping .... *P. dulcis*

15(11). Plants forming shrubby thickets; flowers 14 mm across or less; fruit a plum .... *P. americana*

— Plants treelike or small trees, not forming thickets; flowers 10–30 mm across or more; fruit a cherry 16

16(15). Inner flowerbud scales reflexed or spreading; petals 8–14 mm long; sweet cherry .... *P. avium*

— Inner flower bud scales erect; petals 6–9 mm long; tart cherry .... *P. cerasus*

Prunus americana **Marsh.** American Plum; Pottawattami Plum. Shrubs, often forming thickets, rarely treelike, to 5 m tall; branchlets sometimes thornlike, glabrous; leaves 2.5–7 cm long, 0.5–3 cm wide, elliptic to ovate or lanceolate, sharply serrate, long-attenuate apically, acute to obtuse basally, glabrous or pubescent along veins beneath; petioles usually glandless; flowers 1–4, in sessile or subsessile umbels, from lateral buds, appearing before the leaves, in ours mainly 14 mm broad or less; petals white, 5–7 mm long, 2.5–3 mm wide; sepals spreading, puberulent; hypanthium puberulent without and within; fruit a yellow to red plum. Cultivated fruit plant, and probably indigenous in portions of Utah, but also introduced by pioneers to all areas of the state. The plants spread underground and form thickets that persist. Specimens examined were from Duchesne, Uintah, Utah, and Wayne counties; introduced from central United States; 5 (2).

Prunus armeniaca **L.** Apricot. Small trees to 8 m tall or taller; branchlets green to brown, armed or unarmed; leaf blades mainly 1.5–7 cm long, 1–6 cm wide on mature branches, cordate-ovate to ovate, obtusely serrate, abruptly attenuate, obtuse to cordate basally, glabrous, or hairy along veins beneath; petioles usually with glands; flowers solitary, appearing before leaves; petals white (rarely pinkish), 8–12 mm long, obcordate to orbicular; sepals glandular, the hypanthium glabrous except basally; pedicels villosulose; fruit pubescent, fleshy and edible. Apricot trees are grown in the lower elevation portions of the state, where they escape and persist as waifs along canals, roadsides, and fence rows. Specimens examined are from Beaver, Carbon, Millard, Utah, and Wayne counties; introduced from China; 8 (iii).

Prunus avium **L.** Sweet Cherry. Trees to 8 m tall or taller; branchlets soon brown, unarmed; leaf blades mainly 3–10 cm long, 2.5–8 cm wide, broadly oblanceolate to obovate or elliptic, obtusely serrate to doubly serrate, abruptly short-attenuate, obtuse to rounded basally, glabrous or long-hairy especially along veins beneath; petioles commonly with glands; flowers 2–4 per bud, appearing with early leaves; petals white (rarely pink), 8–14 mm long, obcordate to orbicular; sepals, hypanthium, and pedicels glabrous; fruit glabrous, red to almost black, edible. The Bing, Lambert, Royal Ann, and other cultivars of the sweet cherry are grown commercially and in garden orchards at low elevations in Utah, where frost is not prohibitive. Trees escape from cultivation along canals and in riverbottoms. Many are grown as grafted stock; some on rootstocks of other *Prunus* species, especially on *P. mahaleb* (q.v.). Specimens examined are from Carbon, Utah, and Washington counties; introduced from Eurasia; 4 (0).

Prunus besseyi **Bailey** Western Sand Cherry. Shrubs to 1.3 m tall; branchlets soon brownish, not thornlike; leaf blades mainly 1.5–5 cm long, 0.5–1.8 cm wide, elliptic to oblanceolate, obtusely serrate, acute to cuspidate apically, cuneate basally; glabrous; petioles commonly lacking glands; flowers commonly 2–4 per bud, appearing with early leaves; petals white, 4–6 mm long, 2.5–3.5 mm wide, elliptic; sepals, petals, and hypanthium glabrous; fruit glabrous, black, commonly astringent. The western sand cherry is used as a dwarfing rootstock for peaches, cherries, and other *Prunus* species. The plants persist and escape in orchard areas of the state; erosion control and wildlife plantings are probable; specimens were examined from Utah and Wasatch counties; introduced from the Great Plains; 3 (i).

Prunus cerasifera **Ehrh.** Cherry Plum; Flowering Plum. Small trees to 6 m tall, rarely taller; branchlets soon brown, not thornlike; leaf blades mainly 1.8–6.5 cm long, 1.2–4 cm wide, ovate to elliptic, serrate to doubly serrate, acute apically, acute to rounded basally, villous along the veins beneath; petioles seldom with glands; flowers solitary, or less commonly 2 or 3 per bud; petals pink to violet or white, 6–9 mm long, 4.5–7 mm wide, suborbicular; sepals, hypanthium, and pedicels glabrous, except along marginal insertion of filaments; fruit red to purple, edible. Cultivated ornamentals of streets, lawns, and gardens, persisting and escaping in lower elevation portions of the state; specimens examined from Utah Co.; introduced from Asia; 8 (i). The hybrid between *P. cerasifera* and *P. mume* Sieb. & Zucc., the Japanese apricot is also cultivated in Utah, under the name *P.* x *blireana* Andre. The hybrid has broad purple leaves.

Prunus cerasus **L.** Sour Cherry; Pie Cherry. Small trees to 5 m tall, rarely more; branchlets soon brown, not thornlike; the leaf blades mainly 3–10 cm long, 1.2–5 cm wide, oblanceolate to obovate or elliptic, doubly serrate, abruptly acuminate, acute to rounded basally, glabrous except hairy along veins beneath; petioles bearing glands; flowers commonly 3 per bud (less commonly fewer); petals white, 7–9 mm long and about as broad; sepals crenate-serrate, glabrous; hypanthium and pedicels glabrous; fruit red, soft, sour. This is the tart cherry of commerce, widely cultivated in Utah and a favorite food of robins; specimens examined from Utah Co.; introduced from Eurasia. The species flowers later than does the sweet cherry, and fruit is harvested in mid- to late July, after the sweet cherries have been harvested. The trees long persist; 1 (0).

Prunus domestica **L.** Common or European Plum; Italian Prune. Small trees to 5 m tall, with grayish or ashy bark; branchlets pubescent when young, not especially thornlike; leaf blades mainly 2–10 cm long and 1–6 cm wide, ovate to obovate, coarsely serrate, rough and thinly pubescent above, pubescent beneath; petioles commonly with glands; flowers solitary or sometimes 2 or 3 per bud; petals white, ca 10 mm long; sepals and hypanthium pubescent or glabrous; pedicels commonly pubescent; fruit commonly blue purple, glaucous. Included here are the yellow-fleshed plums known as Damson and Green-Gage, other plums, and the Italian prune. The species is widely cultivated in Utah, where it persists and less commonly escapes. The red-fleshed plums, called Japanese or Satsuma, belong to *P. salicina* Lindl. and are cultivated in the area too, but less commonly; specimens were examined from Beaver and Utah counties; introduced from Eurasia; 4 (i).

Prunus dulcis **(Mill.) D.A. Webb.** Almond. Small trees to 5 m tall or taller; branchlets pale, not thornlike; leaf blades 2–7 cm long, 0.7–2 cm long on mature branches, oblong-lanceolate, crenate-serrate, abruptly short-apiculate, glabrous; petioles usually bearing glands; flowers solitary, appearing before or with early leaves; petals pink; sepals villous at margin; fruit pubescent, splitting at maturity and exposing the stone. Sparingly cultivated ornamental, botanical curiosity, and "nut" tree, known from Utah and Washington counties; persisting, but not escaping (?); introduced from the Old World; 1 (0).

Prunus fasciculata **(Torr.) Gray.** Desert Peach. [*Emplectocladus fasciculatus* Torr.]. Low intricately branched shrub to 1.5 (2) m tall; branchlets pubescent, ashy or grayish, more or less thornlike; leaves mainly 0.5–2.5 cm long, 0.1–0.6 cm wide, cuneate-spatulate, entire or few toothed near the apex, apiculate or cuspidate, sessile or nearly so; not bearing glands at leaf base, more or less puberulent on both sides; flowers mainly 1 per bud; petals cream to white, 3.5–5 mm long, spatulate to elliptic; sepals, hypanthium, and pedicels glabrous; fruit hairy, thin fleshed, inedible. The desert peach occurs in mixed desert shrub and lower pinyon-juniper communities at 625–1770 m in Beaver, Millard, Iron (?) and Washington counties; Arizona, Nevada, and California; 27 (vii).

Prunus laurocerasus **L.** Cherry-Laurel. Evergreen shrub to 2 m, rarely more; branchlets pallid, glabrous, not at all thornlike; leaf blades mainly 3–10 (13) cm long, and 1–3 cm wide, entire or remotely crenate-serrate, elliptic to oblong, attenuate to abruptly so, cuneate to acute basally, leathery-thickened, glabrous; petioles lacking glands; racemes not leafy, commonly 3–10 cm long, many flowered; the pedicels 0.5–1.5 mm long, subtended by large caducous bracts; flowers ca 1 cm wide or less; petals white, 3–4 mm long, obovoid; sepals fringed, glabrous; hypanthium and pedicel glabrous; fruit black, inedible. Cultivated ornamental; specimens from Davis, Utah, and Weber counties; introduced from Eurasia; 8 (0).

Prunus mahaleb **L.** Mahaleb; St. Lucie Cherry. Small trees to 6 m tall or taller; branchlets pale brown, copiously pubescent, not thornlike; leaf blades mainly 2–6 cm long, 1.5–4.5 cm wide, oval to elliptic or ovate, finely crenulate, abruptly acute, acute to rounded basally, commonly glabrous on both sides; petioles sometimes with glands; racemes with 3–12 flowers, corymbose, the axis short, leafy bracted at base; petals white, 4–6 (8) mm long, oblong-oblanceolate; sepals, hypanthium, and pedicels glabrous; fruit black. The Mahaleb Cherry is used as rootstock for other cherry cultivars. It persists and escapes, becoming established along canals and in riverbottom forests in Utah Co.; introduced from Asia; 5 (1). The bitter cherry *P. emarginata* (Dougl.) Walpers is reported for Utah in Vascular Plants of Pacific Northwest 3: 160. 1961, but I have not seen any material of that species from Utah. It would key to *P. mahaleb* in the above key, but differs from inter alia in usually lacking leafy bracts on the peduncle, and in the rounded to obtuse or rarely acute leaves. In some bitter cherry specimens the stems are glabrous and the calyx is hairy. The petals are often pubescent on the dorsal surface, and stones are spindle shaped.

Prunus padus **L.** European Bird Cherry; May Day Cherry. Small trees to 8 m tall, rarely taller; branchlets soon brown, glabrous or puberulent, not thornlike; leaf blades 1.5–20 cm long, 0.7–3.5 cm wide, elliptic to oblanceolate or obovate, serrate, abruptly acuminate, acute to truncate basally, glabrous except sometimes on veins beneath; petioles usually bearing glands; racemes with leafy peduncles, commonly 7–12 cm long, 15- to 25-flowered, the pedicels 5–17 mm long, subtended by caducous bracts; flowers 12–20 mm broad; petals white, 5–7.5 mm long, almost as broad; sepals fringed, glabrous; hypanthium and pedicels glabrous; fruit black, bitter, astringent. Cultivated ornamental of yards and other plantings; Utah Co.; introduced from Eurasia; 1 (0).

Prunus persica **(L.) Batsch.** Peach. Small trees to 3 (4) m tall, seldom more; branchlets green to pallid, becoming ashy in age, glabrous, not thornlike; leaf blades mainly 3–15 cm long (or more), 0.5–5.5 cm wide, oblong-lanceolate to lanceolate, serrate to crenate-serrate, attenuate, obtuse to acute basally, glabrous; petioles usually bearing glands; flowers solitary, appearing before the leaves; petals pink, white, or red; sepals villous at margin; fruit pubescent, fleshy at maturity, edible. Cultivated fruit and ornamental trees at lower elevations in the state, widely escaping along roads; specimens seen from Carbon, Utah, and Salt Lake counties; introduced from China; 8 (i).

Prunus serrulata **Lindl.** Flowering Cherry. Trees to 10 m tall or more; branchlets pallid, becoming brown, glabrous, not thornlike; leaf blades mainly 3–15 cm long, 1.2–8 cm wide, ovate to lance-ovate, abruptly long-acuminate, aristate-serrate, acute to obtuse basally; petioles usually bearing glands; racemes corymbose, 3- to 5-flowered, naked at the base, the pedicels 1.5–30 mm long, each subtended by a cuneate bract fringed at the truncate apex; petals 12–20 mm long, oval, white, rose, pink, often double; sepals glabrous, acuminate or toothed; hypanthium and pedicels glabrous; fruit small, black. This flowering cherry is gaining in popularity, especially in grafted or pendulous forms; specimens examined from Utah Co.; introduced from Japan; 4 (0).

***Prunus tomentosa* Thunb.** Bush Cherry. Shrubs to 2 m tall (commonly lower); branchlets brown, copiously pubescent, not thornlike; leaf blades mainly 2–6 cm long, 1.5–3 cm wide, obovate to elliptic, abruptly acuminate, doubly serrate and obscurely lobed (in some), puberulent above, long-villous beneath; petioles pubescent, not bearing glands; flowers 1 (rarely 2) per bud, appearing before the leaves, sessile or subsessile; petals white or pink, 7–9 mm long, oval; sepals serrulate, pilose; hypanthium glabrous below; fruit red, sparingly pubescent, sour, edible. Cultivated ornamental, escaping and persisting in Utah Co.; introduced from Asia; 4 (0).

***Prunus triloba* Lindl.** Flowering Almond. Shrubs to 2 m (rarely taller); branchlets brown, glabrous; leaf blades commonly 2–5 cm long, 1.5–4 cm broad, ovate to obovate, sharply doubly serrate, pubescent on both sides; flowers 1 or 2 per bud, short-pedicellate; petals pink or white, 8–15 mm long, oval, commonly double; sepals serrulate, glabrous; hypanthium glabrous; pedicels puberulent; fruit red, seldom produced. Sparingly cultivated shrubs, in Salt Lake and Utah counties; introduced from China; 1 (0).

***Prunus virginiana* L.** Chokecherry. Shrubs or small trees to 8 m tall with ashy bark; branchlets brown, glabrous, not thornlike; leaf blades 2–10 cm long, 1.5–7 cm wide, elliptic to oblong-ovate, serrate, abruptly acuminate, acute to rounded basally, glabrous or sometimes pubescent beneath; petioles usually bearing glands; racemes 4–20 cm long, the peduncles usually leafy, 2–8 cm long; flowers 10–20 mm wide, numerous, the pedicels 4–17 mm long, each subtended by a caducous bract; petals white, 4–6 mm long, suborbicular; sepals fringed, glabrous; hypanthium and pedicels glabrous; fruit black when ripe, astringent, edible. Chokecherry fruit has been gathered since early days for making of jelly and syrup, and prior to that by indigenous peoples as a component of pemican. The species is known from all counties in Utah. Our material has been assigned to **var. *melanocarpa* (A. Nels.) Sarg.** [*Cerasus demissa* var. *melanocarpa* A. Nels.; *P. melanocarpa* (A. Nels.) Rydb.; *P. demissa* var. *melanocarpa* (A. Nels.) A. Nels.]. Reports of *P. demissa* or of *P. virginiana* var. *demissa* (Nutt.) Torr. for Utah belong to var. *melanocarpa*. That variety is widely distributed in western North America; 158 (xxvi).

PURPUSIA Brandegee

Plants perennial, caespitose, glandular herbs, arising from a caudex; leaves mainly basal, pinnately compound; flowers perfect, regular, borne in few-flowered cymes; hypanthium campanulate to turbinate, usually lacking bractlets; sepals 5; petals 5, white to yellowish; stamens 5, opposite the sepals; pistils mostly 6–12, on a stalked receptacle; fruit of achenes.

***Purpusia saxosa* Brandegee** [*P. arizonica* Eastw.; *P. osterhoutii* A. Nels.; *Potentilla osterhoutii* (A. Nels.) J. T. Howell]. Perennial glandular herbs from a caudex, the stems 0.5–2 dm tall; basal leaves pinnate with 5–11 leaflets, the leaflets 0.5–1.5 cm long, broad, deeply toothed or cleft; sepals 2.5–3 mm long, lance-ovate, acuminate; petals yellow or white, 3–4 mm long, oblanceolate, acuminate; achenes on a receptacle 1.5–2 mm long. This species is included in Utah on the basis of a collection reported by Meyer (1976) taken at Kolob Reservoir, Washington Co.; Arizona, Nevada, and California; 0 (0).

PURSHIA DC. ex Poir.

Shrubs with unarmed branches; leaves alternate, simple, apically 3-toothed, usually glandular; stipules triangular-attenuate, persistent; flowers perfect, regular, solitary, on short lateral spur branchlets; sepals 5, borne atop a turbinate-funnelform persistent hypanthium; petals 5, yellow; stamens ca 25; pistils 1 or 2, borne on a stipe at base of hypanthium; fruit an achene.

1. Leaves with conspicuously punctate, depressed glands, glabrous above; plants of Washington Co. .... *P. glandulosa*

— Leaves lacking punctate depressed glands, puberulent above; plants widespread .... *P. tridentata*

Purshia glandulosa **Curran** Shrubs, much branched, 1–2 (3) m tall; branchlets prominently glandular; leaves 3–10 mm long, 1- to 4-mm wide, cuneate, glabrous above, slightly tomentose beneath, the margins revolute; hypanthium glabrous to tomentose, 2.5–5 mm long, funnelform; petals 4–8 mm long, spatulate, creamy white to yellowish; achenes oblique, ca 2 cm long, including style, puberulent. Blackbrush, chaparral, and pinyon-juniper communities at 1065 to 1375 m in Washington Co.; Nevada, Arizona, and California; 2 (i).

Purshia tridentata **(Pursh) DC.** Bitterbrush. Shrubs, much branched, to 2 m tall (rarely taller); branchlets brown, tomentulose; leaves mainly 4–20 mm long, 2–12 mm wide, cuneate, apically 3 (5) -toothed, tomentose but green above, grayish tomentose beneath, the margins more or less revolute; hypanthium tomentose and stipitate glandular; sepals mainly 4–6 mm long, ovate-oblong, entire; petals 5–9 mm long, oblong to obovate or spatulate, yellow; achenes obliquely ovoid, 1–2 cm long, the beak about one-third the length, puberulent. Bitterbrush is a plant of sagebrush, mountain brush, pinyon-juniper, and ponderosa pine communities at 1220 to 2775 m in all counties in Utah; British Columbia east to Montana and south to California, Arizona, and New Mexico. This species forms hybrids with *Cowania mexicana*; such plants are distinguished by the more lobed leaves, and longer and more numerous achenes; 122 (xi).

PYRACANTHA Roem.

Evergreen shrubs, armed with thorns; leaves alternate, simple, crenate-serrate, petiolate; stipules minute, caducous; flowers perfect, regular, borne in simple or branched corymbs; sepals 5; petals 5, white; stamens 20, the filaments subulate; pistil 1, the ovary inferior, 5-loculed; styles usually 5; fruit a pome.

Pyracantha coccinea **Roem.** Fire-thorn. Shrubs to 3 m tall or more, with thorns 0.5–1.5 cm long or more; leaf blades 0.8–4.5 cm long, 0.5–1.8 cm wide, elliptic to oblanceolate, acute apically, cuneate to acute basally, crenate-serrate; petioles puberulent; inflorescence pilosulous at anthesis; sepals broadly triangular; petals white, 3–4 mm long, 2–3 mm wide; pomes red orange, persistent. The fire-thorn is a common plant in cultivation through much of Utah; the plants persist following cultivation and escape rarely; Utah Co.; introduced from Eurasia; 6 (0).

PYRUS L.

Trees with unarmed branches; leaves alternate, simple, not or seldom lobed; stipules deciduous; flowers perfect, regular, borne in corymbs; hypanthium short; sepals 5, persistent; petals 5, white; stamens many; pistil 1, the ovary inferior, usually 5-loculed; styles 3–5, separate to the base; fruit usually pear shaped, the flesh with stone-cells.

Pyrus communis **L.** Common pear. Small trees to 6 m tall, the branchlets commonly glabrous; leaves 2–8 cm long, ovate to oblong or elliptic, glabrous or glabrate, leathery, crenate-serrulate to subentire; flowering with the leaves; petals white, mainly 12–18 mm long; fruit pear shaped to almost spherical. The pear of commerce is widely grown in Utah, with Bartlett being the most common cultivar; 8 (ii).

ROSA L.

Shrubs, deciduous; stems armed with prickles or spines, rarely unarmed; leaves alternate, pinnately 3- to 9-foliolate; stipules conspicuous, adnate to petioles; flowers perfect, solitary or in corymbs; hypanthium urn shaped to globose or ellipsoid, red, red orange, yellow, or purplish, fleshy at maturity; sepals 5; petals 5 (or numerous in double forms); stamens numerous, inserted on margin of ringlike disk; pistils few to numerous; styles exserted through or to orifice of disk;

fruit of achenes, enclosed in the fleshy hypanthium (hip). The cultivated roses are largely of hybrid derivation, and are not well represented in herbaria. The key includes both indigenous and cultivated taxa because of the propensity of some species to escape and of others to persist for long periods following cultivation. The key is tentative at best, because of the propensity of all roses to hybridize.

1. Stipules deeply fringed or pectinate, appearing as lateral projections of petiole base; flowers white (or pink in some hybrids keying here); cultivated and escaping .... *R. multiflora*
— Stipules entire, or rarely fringed, but not cut to the petiole; flowers variously colored 2
2(1). Flowers mostly 5–9 cm broad; styles long-exserted from hypanthium; cultivated and persisting .... *R. odorata*
— Flowers mostly less than 5 cm broad; styles not exserted, forming a dense headlike stopper in orifice of hypanthium 3
3(2). Leaflets stipitate-glandular beneath; sepals strongly stipitate-glandular, erect or spreading in fruit; cultivated and escaping .... *R. rubiginosa*
— Leaflets not at all or only sparingly stipitate-glandular beneath; sepals various in fruit; cultivated and escaping or indigenous 4
4(3). Sepals reflexed and finally deciduous after flowering; stipitate glands sparse on lower midveins and sepals; cultivated and escaping .... *R. canina*
— Sepals erect and persistent following flowering; stipitate glands rarely present; plants indigenous 5
5(4). Sepals 1.5–4 long; petals 2.2–4 cm long; hips 1–2 cm long at maturity ..... *R. nutkana*
— Sepals 1–2.2 cm long; petals 1–2.5 cm long; hips 0.6–1.5 cm long at maturity .... *R. woodsii*

***Rosa canina* L.** Dog Rose. Shrub 1–3.5 (4) m tall; stems sometimes clambering, armed with scattered, strongly curved to straight spines and no prickles, glabrous; stipules entire; leaves 3–8 cm long or more, with 3–7 leaflets, the terminal leaflet 0.6–2.2 cm long, 0.3–1.2 cm broad, glabrous to sparingly villous and stipitate-glandular along the veins beneath, serrate to doubly serrate; flowers single, solitary or 2–5 on short glabrous or glandular pedicels; sepals 1.2–1.5 cm long, sparingly stipitate-glandular, reflexed in fruit, soon shattering; petals white or pink, 1–1.8 cm long; hips ovoid, about 1 cm thick, red. Cultivated, persisting, and rarely escaping in lower elevation portions of Utah, specimens examined from Utah and Salt Lake counties; introduced from Europe.

***Rosa multiflora* Thunb.** Multiflora Rose. Shrub to 2 or 3 m tall or more; stems sometimes clambering, armed with prickles or rarely unarmed, glabrous; stipules about half as long as the petiole, pectinate, cut almost to petiole; leaves 4–9 cm long or more, 5- to 11-foliolate, the terminal leaflet 1.5–3 cm long, glabrous or puberulent and rarely with some glands beneath, serrate; flowers numerous (to 50 or more), white (pink in some hybrids), single (double); sepals reflexed in fruit, pubescent; petals 5, or numerous, 0.6–0.8 cm long; hips ovoid, about 6 mm thick, brownish red. Herbarium specimens are very few for this species in Utah, and those involve hybrids with other species and are only tentatively placed herein; Utah Co.; introduced from Japan; 3 (0).

***Rosa nutkana* Presl.** Nutka Rose. [*R. spaldingii* Crepin]. Shrubs 0.3–2 m tall, rarely more; stems erect or ascending, armed with distinctive infrastipular spines (or rarely unarmed), the internodal prickles lacking or few and different from the infrastipular spines; leaves 6–13 cm long, with 5–7 (9) leaflets, the terminal one 1–7 cm long, 0.8–3.5 cm broad, pubescent to glabrous, rarely stipitate-glandular beneath, serrate to doubly serrate; flowers solitary (rarely 2 or 3); sepals 1.5–4 cm long, 3–6 mm wide; petals 5, pink, 2.2–4 cm long; hips ellipsoid to subglobose, 1–2 cm long and thick, red orange to purplish. Oak-maple, aspen, mountain brush, sagebrush, Douglas fir, cottonwood, and spruce-fir communities at 1525 to 3355 m in Beaver, Box Elder, Carbon, Duchesne, Garfield, Grand, Juab, Millard, Piute, Salt Lake, Sanpete, Summit, Tooele, and Utah counties; Alaska south to California, Nevada, and Colorado. The features of larger fruit, longer and broader sepals, and usually solitary flowers are diagnostic when taken in combination for most specimens. However, intermediate specimens between Nootka and Woods rose are known. Our material has been assigned to var. *hispida* Fern.; 48 (vii).

Rosa odorata **Sweet.** Tea Rose; Hybrid Rose. Shrubs, 0.3–6 m long or more; stems erect or ascending to clambering, armed with infrastipular and/or internodal spines or prickles, or unarmed; leaves 4–20 cm long, with usually (3) 5 leaflets, the terminal 1–7 cm long, 0.8–4 cm wide, once or twice serrate, glabrous or pilose and somewhat stipitate glandular; flowers solitary or usually few to numerous; petals 5, or more commonly numerous, of various colors and sizes; hips various in size, shape, and color. Included within this catchall name are the hybrid tea roses of commerce, grown widely in Utah for ornament. The cultivars are mainly complex hybrids, with ancestors involving *R. moschata* J. Herrmann, *R. foetida* J. Herrmann, *R. gallica* L., *R. chinensis* and *R. multiflora* Thunb. (see Flora Europaea, 1968, p. 26 for a more complete discussion). The hybrid roses persist and are present around abandoned farmsteads in Utah; introduced from Eurasia; 3 (i).

Rosa rubiginosa **L.** Sweetbriar. [*R. eglanteria* L.]. Shrubs 0.5–2 m tall; stems erect or ascending, armed with distinctive flattened infrastipular spines and often with straight internodal prickles; leaves 3.5–10 cm long, with 5–7 (9) leaflets, the terminal one 1.2–3.5 cm long, 0.8–3 cm wide, conspicuously stipitate glandular on one or both surfaces; doubly serrate; flowers solitary or 2–4; sepals 1–2 cm long; petals 0.8–2 cm long, pink to white; hips 1–1.5 cm long, ellipsoid to subglobose. Cultivated, persisting, and escaping in Salt Lake and Tooele counties, and likely elsewhere in Utah; introduced from Utah; 2, 0.

Rosa woodsii **Lindl.** Woods Rose. [*R. fendleri* Crepin; *R. neomexicana* Cockerell; *R. manca* Greene; *R. arizonica* Rydb.; *R. californica* var. *ultramontana* Wats.; *R. macounii* Greene; *R. chrysocarpa* Rydb., type from Abajo Mts.; *R. puberulenta* Rydb., type from Montezuma Canyon]. Shrubs 0.1–2.5 (3) m tall; stems armed with infrastipular spines and/or internodal prickles or spines, or unarmed; leaves 1.5–13 cm long, 0.4–2.5 cm broad, pubescent to glabrous and rarely stipitate glandular, serrate to doubly serrate; flowers solitary or 2 to several; sepals 1–2.2 cm long, 2–3.5 cm wide; petals 5, pink (rarely white), 1–2.5 cm long; hips ellipsoid to subglobose, 0.6–1.5 cm long and thick, red orange to yellow. Streamsides, irrigation canals, marsh lands, lake shores and hillsides in palustrine, lacustrine, and riparian habitats; also in mountain brush, juniper, aspen, and spruce-fir communities at 850 to 3265 m in all Utah counties; Alaska and MacKenzie east to Hudson Bay and south to California, Texas, Missouri, and Wisconsin. The species is represented in Utah by a variable assemblage that has been included within the concept of var. *ultramontana* (Wats.) Jeps. There are plants from Garfield and San Juan counties especially, which have very coarse internodal as well as infrastipular spines. These would key to *R. neomexicana* Cockerell, but gradient specimens tie these striking exceptions to the mass of variation within the complex of forms. The striking species ***R. stellata*** **Woot.** might occur in southern Utah. The young stems of that species are stellate-pubescent or copiously glandular hispidulous or both, and the older stems are armed with numerous long, nearly straight prickles; 140 (xv).

Rubus L.

Shrubs; stems armed with prickles or bristles, or unarmed; leaves alternate, pinnately compound or palmately veined and lobed; stipules various, usually persistent; flowers perfect or imperfect, regular, solitary or few to numerous in cymes; hypanthium short, saucerlike, lined with a glandular disk; sepals usually 5, lacking bracteoles; petals the same number as the sepals; stamens 15 to numerous, linear-subulate; pistils several to many, the ovaries superior, each 1-loculed; styles 1 per pistil, the stigma capitate; fruit of separate drupelets, or the drupelets coherent and free of the receptacle, hence an "aggregate" fruit.

BAILEY, L. H. 1941. Species Batorum. The genus *Rubus* in North America. Gentes. Herb. 5: 1–932.

1. Leaves simple, palmately veined and lobed, green on both sides; stems unarmed 2

— Leaves compound pinnately 3 to 5 foliolate; stems armed 3

2(1). Leaves mainly less than 6 cm wide, the lobes rounded in general outline, green above, white-tomentose beneath; flowers mainly solitary, plants rare, known only from low elevations in San Juan Co. .... *R. neomexicana*

— Leaves mainly 6–30 cm wide, the lobes acute to attenuate in general outline; flowers borne in clusters of 2–6 or more plants locally common, montane, widespread .... *R. parviflorus*

3(1). Main prickles straight, slender, retrorsely disposed along stem; fruit red when ripe .... *R. idaeus*

— Main prickles flattened, curved or straight, retrorse or retrorsely curved 4

4(3). Receptacle fleshy, the drupelets adhering, not slipping free when ripe; stems usually strongly armed, trailing or clambering; cultivated, persisting, and escaping .... *R. discolor*

— Receptacle not fleshy, the drupelets slipping free when ripe; stems arching, but not trailing or clambering; indigenous and with cultivated phases .... *R. leucodermis*

Rubus discolor **Weihe & Nees** Himalayan Blackberry. [*R. procerus* Muell.-Arg.]. Shrubs, often clambering or sprawling, the stems to several m long, armed with strong, straight, flattened spines; stipules linear, entire; leaves 7–20 cm long, pinnately to palmately compound, with 3–5 leaflets, the terminal leaflet 3–12 cm long, 2–8 cm wide, green and glabrous above, tomentose beneath; flowers usually perfect, conspicuous, mainly 3–20 in clusters; sepals 6–10 mm long, lanceolate; petals white (rarely reddish), 10–15 mm long; staminal filaments linear; pits to 3 mm long, the drupelets adherent to receptacle, numerous, the flavor agreeable. Roadsides, field margins, and abandoned farmsteads in Juab, Utah, and Washington counties (likely elsewhere); introduced from the Old World; 3 (i).

Rubus idaeus **L.** Raspberry [*R. strigosus* Michx.; *R. idaeus* var. *strigosus* (Michx.) Maxim.; *R. sachalinensis* H. Levl.; *R. idaeus* ssp. *sachalinensis* (H. Levl.) Focke; *R. idaeus* var. *canadensis* Richards.; *R. melanolasius* Dieck]. Shrubs, 2–15 (20) dm tall, the stems, petioles, and veins on lower leaf surfaces with glandular pricklelike processes or prickles, or both; stipules linear; leaves 2–20 cm long, pinnately compound with 3–5 leaflets, the terminal leaflet 1.2–10 cm long, 0.6–7.5 cm broad, green and glabrous to hairy above, white or gray hairy to glabrate and greenish beneath; flowers perfect, not conspicuous, solitary or 1 to few in clusters; sepals 4–12 mm long, lanceolate; petals white, 4–7 mm long; staminal filaments slender, often somewhat clavate; pits 2–2.5 mm long, the drupelets coherent, red, several to many, the flavor agreeable. Riparian sites and talus slopes in aspen and mixed conifer communities at 2135–3420 m in Beaver, Carbon, Duchesne, Emery, Garfield, Grand, Iron, Juab, Kane, Piute, Salt Lake, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, and Washington counties; Alaska east to the Atlantic and south to California, Mexico, Iowa, and North Carolina; Eurasia. Our indigenous ma terial belongs to ssp. ***melanolasius*** **(Dieck) Focke.** Cultivated phases belong mainly to ssp. *idaeus*; 48 (xiii).

Rubus leucodermis **Dougl. ex T. & G.** Black Raspberry. Shrubs, mainly 1–3 m long, the stems, petioles and some veins on lower leaf surfaces armed with retrorsely curved, flattened, catclawlike prickles; stipules linear; leaves 6–14 cm long, pinnately compound, with 3–5 leaflets, the terminal leaflet 3–7.5 cm long, 2–6 cm wide, green and almost or quite glabrous above, white-tomentose beneath; flowers usually perfect, not conspicuous, mainly 2–10 in clusters; sepals 6–12 mm long, lance-acuminate; petals white, shorter than the sepals; staminal filaments slender, linear-subulate; pits to 2.5 mm long, the drupelets coherent, several to many, the flavor agreeable. Dry open slopes in mountain brush and in riparian communities at 1678 to 2200 m in Millard, Salt Lake, and Utah counties; British Columbia east to Montana and south to California and Nevada. The plants are rare in collections, and the distribution is probably wider than indicated; 4 (0).

Rubus neomexicanus **Gray.** Shrubs, 0.5–1.5 m tall, the stems, petioles, and leaves unarmed, merely villous-puberulent and sometimes minutely glandular; stipules lance-ovate, entire or serrate; leaves palmately lobed and veined, simple, the blades 1.2–4.2 cm long (from sinus to apex), 1.5–5.5 cm wide, green above, pale green beneath, puberulent on one or both sides; flowers usually perfect, solitary, showy; sepals 10–14 mm long, lance-ovate, entire or serrate; petals white, 2–17 mm long, the drupelets not especially coherent, red, several to many, thinly fleshed, hardly palatable. Hanging garden with *Ostrya knowltonii*, at 1130 to 1160 m in Ribbon Canyon, San Juan Co., and to be sought in other shaded moist alcoves along Lake Powell; Arizona and New Mexico. This is a truly attractive species, with startling large white roselike flowers; 5 (iii).

Rubus parviflorus **Nutt.** Thimbleberry. Shrubs, 0.5–2 m tall, rarely taller, the stems, petioles, and leaves unarmed, stipitate-glandular; stipules lanceolate, entire or serrate; leaves palmately lobed and veined, simple, the blades 4.5–15 cm long (from sinus to apex), 5.5–20 cm wide, green above, pale beneath, puberulent on one or both sides, or glabrate above; flowers usually perfect, in clusters of 2–7, showy; sepals 8–19 mm long, ovate, the apex caudate-attenuate, entire; petals white, 13–18 (20) mm long, or more; staminal filaments linear-subulate; pits to 3 mm long, the drupelets coherent as an aggregate, red, numerous, thinly fleshy, almost dry at maturity, palatable. Riparian habitats in aspen, spruce, fir, lodgepole, Douglas fir, mountain brush at 1435 to 2745 m in Duchesne, Salt Lake, San Juan, Sanpete, Summit, Tooele, Utah, Wasatch, and Weber counties; Alaska east to Great Lakes, and south to California, Arizona, New Mexico, and the Dakotas. Our plants belong to var. ***parviflorus***; 25 (i).

SANGUISORBA L.

Perennial herbs, from a branching caudex; leaves basal and alternate, pinnately compound; stipules adnate to the petioles, persistent; flowers mostly imperfect, regular, numerous in short to elongate, dense spikes; hypanthium subglobose, restricted near the apex; sepals 4, petaloid; petals lacking, stamens numerous; pistils 1–3, the ovary superior, 1-loculed; styles 1 per pistil, the stigma capitate, fringed; fruit an achene, enclosed by the usually 4-angled to 4-winged hypanthium.

Sanguisorba minor **Scop.** Burnet. Plants mainly 2–5 dm tall; caudex clothed with persistent stipules and petioles; basal leaves 4–18 cm long, with mostly 9–17 oval to obovate-oblong leaflets, 0.6–1.8 cm long, coarsely serrate; spikes subglobose to cylindroid, 8–40 mm long; bractlets ovate; flowers mainly imperfect, the lower staminate and the upper pistillate; calyx greenish or pinkish; hypanthium cone shaped in fruit, woody; stamens numerous, the filaments filiform, long-exserted. Introduced revegetation and erosion control plant at 1525 to 2135 m elevation in Garfield, Tooele, Utah, and Washington counties; introduced from Europe; 7 (ii).

SIBBALDIA L.

Perennial herbs from a caudex; leaves basal or cauline and alternate, long-petioled, palmately 3-foliolate; stipules adnate to petioles, persistent, lanceolate; flowers perfect, regular, borne in leafy-bracted cymes; hypanthium short, saucer shaped, lined with a glandular disk; sepals 5, alternating with 5 sepaloid bracteoles; petals 5; stamens usually 5; pistils 5–20, distinct, the ovaries superior; styles 1 per pistil, the stigmas capitate; fruit an achene.

Sibbaldia procumbens **L.** Sibbaldia. Plants low, mat forming, the flowering stems 0.4–1.4 dm tall; leaves 2–12 cm long, the 3 leaflets oblanceolate to obovate, 3 (rarely 5)-toothed apically, the terminal leaflet 11–32 mm long, 7–18 mm broad, stiffly hairy on both surfaces; flowers inconspicuous; sepals 2.5–5 mm long; petals pale yellow, 1.5–3 mm long; achenes stipitate, about 1 mm long. Alpine tundra, krumholz, spruce-fir, meadow, and lodgepole pine communities, often in talus or gravel at 2745 to 3660 m in Beaver, Daggett, Duchesne, Grand, Piute, Summit, Uintah, Utah, and Wayne counties; Alaska east to Newfoundland and south to California, Colorado, Quebec, and New Hampshire; circumboreal; 28 (vi).

SORBARIA (Ser.) A. Br.

Shrubs with unarmed branches; leaves alternate, pinnately compound; stipules persistent; flowers perfect, regular, borne in terminal panicles; hypanthium short, lined with a glandular disc; sepals 5, persistent; petals 5, white; stamens 20–50; pistils 5, somewhat connate basally; styles 1 per pistil, the stigmas capitate; fruit of follicles.

Sorbaria sorbifolia **(L.) A. Br.** Sorbaria. Shrubs to 2 m tall, sometimes taller; leaves 8–20 cm long or more; leaflets 11–23, lanceolate to oblong-lanceolate, serrate or doubly so, long-acuminate, glabrous or puberulent, the hairs stellate; inflorescence 10–25 cm long; flowers white, about 8 mm wide; hypanthium glabrous; fruit glabrous. Cultivated ornamental in Davis, Salt Lake, and Utah counties, and probably elsewhere; introduced from Asia; 4 (0).

SORBUS L.

Shrubs or small trees with unarmed branches; leaves alternate, pinnately lobed or compound; stipules persistent or deciduous; flowers perfect, regular, numerous in corymbose cymes; hypanthium short, lined with a glandular disk; sepals 5, persistent; petals 5, cream to white; stamens 15–20; pistils 1, the ovary inferior, 2- to 5-loculed; styles 2–5, the stigmas capitate; fruit a pome.

JONES, G. N. 1939. A synopsis of the North American species of *Sorbus*. J. Arnold. Arb. 20: 1–43.

1. Leaves simple, lobed or pinnatifid; petioles and branchlets of inflorescence densely white villous-tomentose .... *S. hybrida*
— Leaves compound; petioles and branchlets of inflorescence sparingly tomentose 2
2(1). Winter buds densely white-villous, the surface obscured by the hairs; maximum leaflet number commonly 15; plants cultivated .... *S. aucuparia*
— Winter buds sparingly hairy, the shiny surface not at all obscured by the hairs; maximum leaflet number 13; plants indigenous .... *S. scopulina*

Sorbus aucuparia **L.** European Mountain-ash. Trees, mostly 3–6 m tall, with grayish or yellowish green smooth bark; winter buds densely white-villous; leaves pinnately compound; leaflets 11–15, 3–5 cm long, 1–1.8 cm broad, the margins coarsely serrate except at the base; petioles and branches of inflorescence sparingly white-hairy at least in flower; stipules persistent; flowers 8–10 mm broad; sepals triangular; petals white to cream, orbicular, 3–4.5 mm long; fruit 9–11 mm long, scarlet, drying purplish. Cultivated ornamental, persisting, and escaping (?) in Salt Lake, Summit, and Utah counties; introduced from Europe; 11 (0).

Sorbus hybrida **L.** Trees, mostly 3–6 m tall, with grayish or yellowish green smooth bark; winter buds white-villous-tomentose; leaves simple or pinnatifid, usually with at least one pair of lobes free at base of blade, the lobes coarsely serrate or doubly serrate; petioles and branches of inflorescence densely white, villous-tomentose; stipules deciduous; flowers 10–14 mm broad; sepals triangular; petals white to cream, broadly elliptical 5–6 mm long; fruit 10–12 mm long, globose, red. Cultivated ornamental, persisting, in Utah county; introduced from Europe; 7 (0).

Sorbus scopulina **Greene.** Shrubs, 1–4 m tall, with grayish-red or yellowish bark; winter buds glutinous and glossy, white-hairy to glabrous; leaves pinnately compound; leaflets 7–13, 2–9 cm long, 0.7–3 cm broad, sharply serrate almost to the base; branches of inflorescence sparingly to rather densely pubescent with white hairs; stipules persistent or tardily deciduous; flowers 8–12 mm broad; sepals triangular; petals white to cream, oval, 4–6 mm long; fruit 5–10 mm long, scarlet to orange, drying purplish. Aspen, spruce-fir, white fir, Douglas fir, and ponderosa pine communities at 2075 to 2900 m in Carbon, Duchesne, Salt Lake, San Juan, Sanpete, Summit, Utah, Wasatch, Washington, and Weber counties; Alaska south to California, New Mexico, and the Dakotas; 28 (vi).

Spiraea L.

Deciduous shrubs with unarmed branchlets; leaves alternate, simple; stipules obsolete; flowers perfect, regular, borne in terminal corymbs; hypanthium cup shaped; sepals 5, persistent; petals 5; stamens 25 or more; pistils 3–7 (usually 5), distinct, the ovaries superior, each 1-loculed; styles 1 per pistil, the stigmas capitate; fruit a few-seeded follicle.

Spiraea* x *vanhouttei **(Briot) Zabel.** Shrubs to 2 m tall; stems finally arching; leaves 0.8–3.5 cm long, 0.4–1.7 cm wide, cuneate-obovate, serrate to doubly serrate at the apex and often 3- to 5-lobed; inflorescences pedunculate, terminal on short lateral branches; petals white, 3.5–4.5 mm long, oval; follicle to 5 mm long (including styles). Commonly cultivated ornamental, persisting in Carbon, Salt Lake, and Utah counties; introduced from Eurasia. This plant a hybrid involving S. *cantoniensis* Lour. and S. *trilobata* L.; 5 (0).

SEASONAL FOODS OF COYOTES IN SOUTHEASTERN IDAHO: A MULTIVARIATE ANALYSIS

James G. MacCracken[1,2] and Richard M. Hansen[1]

Abstract.— Seasonal foods of coyotes (*Canis latrans*) inhabiting the Idaho National Engineering Laboratory site were examined using step-wise discriminant analysis. Significant differences ($P < 0.01$) were detected among seasons in food consumption by coyotes, where univariate statistical analysis failed to recognize differences. Recognition of seasonal changes in foods consumed by coyotes is essential to understanding coyote feeding strategies. The role opportunistic behavior plays in coyote food selection on the study area is questioned.

Coyotes (*Canis latrans*) have been and continue to be a center of controversy (Bailey 1907, Taylor et al. 1979). As a result, numerous studies have been published dealing with many aspects of coyote ecology (Bekoff 1978). Food habits of coyotes are well documented in the literature for a variety of ecological conditions (Murie 1935, Clark 1972, MacCracken 1981). Few studies, however, have evaluated coyote foods on a seasonal basis (Meinzner et al. 1975). Although many studies have shown that one or two items make up the bulk of coyote foods (Sperry 1941, Murie 1945, Gier 1968, Johnson and Hansen 1979a, and others), the relative abundance of these prey species experiences seasonal fluctuations. The seasonal availability and abundance of some food items would presumably result in seasonal differences in coyote diets if coyotes are truly opportunistic feeders. Johnson and Hansen (1979a) and MacCracken (1981) both questioned the degree opportunistic behavior plays in coyote feeding.

In the past, discussion of seasonal differences in coyote foods has largely been based on observed changes of relative amounts of a single item in a coyote dietary. Statistical analysis has been limited due to the number of variables (food items) involved, violation of assumptions of univariate tests, and the lack of a test's power in detecting differences.

The purpose of this paper is to present data on seasonal coyote foods in southeastern Idaho and to discuss the application of a multivariate procedure in detecting differences in coyote food selection.

Study Area and Methods

This study was conducted on the Idaho National Engineering Laboratory (INEL) site in southeastern Idaho from October 1977 through July 1979. Johnson and Hansen (1979a) studied coyote food habits on the INEL site from July 1975 to July 1977. The INEL site was located on the Upper Snake River Plain, which is dominated by sagebrush-grass vegetation associations (Harniss and West 1973, Anderson and Holte 1981). Eggler (1941) gave a description of the geology and climate of the plain.

The INEL site was divided into two areas based on the presence or absence of coyote control programs. Control activities were confined to the peripheral portion of the INEL site. Livestock grazing was also confined to the peripheral portion of the study area.

Coyote feces were collected from 25 permanent transects systematically located as described by Johnson and Hansen (1979a). We included transitional areas defined by Johnson and Hansen as being part of the central area in this study. Transects were gleaned of all coyote feces in July 1977. Coyote feces examined in this study were collected in October 1977 and 1978, representing summer diets, in December 1977, representing fall food consumption, June 1978 and April 1979, representing primarily winter diets, and July 1979, which represented a period of spring feeding by coyotes.

---

[1] Department of Range Science, Colorado State University, Fort Collins, Colorado 80523.

[2] Present address: USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station, Rapid City, South Dakota 57701.

Coyote feces were dried at 60 C for 48 hours in a forced-air-drying oven, then weighed. Each dried scat was placed in a fine mesh nylon bag, soaked for 24 hours in tap water, then cleared of all soluble material by agitating in a clothes washer. After all soluble material had been removed, scats were tumbled dry in a clothes drier.

Food items in scats were identified by comparison with reference materials and recorded by frequency of occurrence. Frequency of occurrence of food items was converted to grams of dry matter ingested following procedures explained by Johnson and Hansen (1979b).

An estimate of coyote food consumption was determined for each of the 25 transects for each collection date. Five diet estimates were randomly selected for analysis, using a table of random digits (Snedecor and Cochran 1967) for each collection date and both areas of the INEL site, which included approximately 550 feces.

Differences in coyote food consumption among seasons were tested for significance with step-wise discriminant analysis (Hope 1968, Cooley and Lohnes 1971, Klecka 1975). Discriminant analysis determined which variables (food items) were the most useful in distinguishing between seasons, developed equations (discriminant functions) that classified diet estimates as to season of feeding, and indicated which variables contributed the most information to a particular function.

Results

Nuttall cottontails (*Sylvilagus nuttali*), montane voles (*Microtus montanus*), and northern pocket gophers (*Thomomys talpiodes*) made up the bulk of coyote foods during the period of this study (Table 1). Significant differences ($P < 0.01$) were detected among seasons in coyote food consumption as each variable was entered into discriminant analysis. All seasonal diets were different ($P < 0.01$) after 15 of 21 food items had been considered. Those 15 food items were the

Table 1. Mean (± SE) percent relative dry weight (g) of food items recovered from coyote feces collected on a seasonal basis from the Idaho National Engineering Laboratory. Number of diet estimates is in parentheses.[1]

Food items	Season			
	Winter(12)	Spring(14)	Summer(22)	Fall(12)
Mammals				
Sylvilagus nuttalli	32 ± 8	40 ± 8	69 ± 5	61 ± 6
Brachylagus idahoensis	4 ± 4	13 ± 5	2 ± 1	2 ± 2
Lepus californicus	9 ± 5	°	1 ± 1	4 ± 2
L. townsendi	1 ± 1	2 ± 1		
Microtus montanus	12 ± 5	16 ± 6	11 ± 3	7 ± 3
Thomomys talpoides	3 ± 2	11 ± 4	4 ± 2	4 ± 2
Perognathus sp.	1 ± 1	1 ± 1	5 ± 2	1 ± 1
Cricetid mice	3 ± 2	1 ± 1	1 ± 1	7 ± 4
Antilocapra americana	3 ± 2	1 ± 1	1 ± 1	7 ± 3
Livestock	11 ± 6		1 ± 1	
Spermophilus townsendi	1 ± 1	9 ± 3	°	2 ± 1
Dipodomys ordi	6 ± 4	1 ± 1	°	1 ± 1
Eutamias minimus		2 ± 1		2 ± 2
Marmota flaviventris	3 ± 3			
Neotoma cinerea	1 ± 1			
Birds	1 ± 0	2 ± 1	1 ± 1	°
Reptiles	°		2 ± 1	°
Insects	4 ± 4	1 ± 0	1 ± 0	°
Seeds	°	°	°	°
Plant fragments	1 ± 0	°	°	1 ± 0
Grass macrofragments	5 ± 5	°	°	

°<1%

[1] Diet estimates were derived from many feces. A total of 550 feces were analyzed.

most useful in differentiating among seasonal diets of coyotes and accounted for 95 percent of data variation. Those food items, in order of significance, were: Townsend ground squirrels (*Spermophilus townsendi*), Nuttall cottontails, pygmy rabbits (*Brachylagus idahoensis*), plant fragments, pronghorn (*Antilocapra americana*), pocket mice (*Perognathus* sp.), bushy-tailed woodrats (*Neotoma cinereus*), reptiles, whitetail jackrabbits (*Lepus townsendi*), montane voles, Cricetid mice, northern pocket gophers, birds, least chipmunks (*Eutamias minimus*), and macrofragments of grass. Plant fragments were from prey stomachs, and grass macrofragments were leaves directly consumed by coyotes.

Certain food items were associated with a season of feeding by coyotes as revealed by examination of discriminant classification function coefficients (Table 2). Birds, Townsend ground squirrels, plant fragments, and bushy-tailed woodrats contributed information during all seasons; however, the additional occurrence of reptiles in coyote scats was indicative of summer diets, pronghorn of fall diets, macrofragments of grass winter diets, and whitetail jackrabbits of spring diets. All food items were positively associated with seasonal diet selection, except bushy-tailed woodrats.

Other food items also exhibited differences ($P < 0.01$) in seasonal consumption by coyotes, but contributed relatively little information to explained variation. Insects, Ord's kangaroo rats (*Dipodomys ordi*), livestock, and yellow-bellied marmots (*Marmota flaviventris*) occurred most frequently in winter scats.

Discussion

Coyote food selection during the period of this study was similar to that reported by Johnson and Hansen (1979a). Johnson and Hansen (1979a), however, did not report any significant differences in coyote foods among seasons when comparing means with a student's *t*-test. MacCracken (1980) lumped coyote foods into five categories (leporids, rodents, ungulates, birds, and insects) and tested for differences among collection dates with factorial analysis of variance. This procedure also failed to detect significant differences in seasonal occurrence of coyote foods. Discriminant analysis has value in the treatment of food habits data in that all food items can be evaluated and significant changes in food consumption are detectable.

Lehner (1976) stated that knowledge of coyote feeding strategies could be useful in altering the role livestock and game animals play in those strategies. To fully understand coyote feeding strategies, wildlife managers and researchers must consider seasonal changes in food consumption by coyotes and be able to determine which food items

Table 2. Discriminant classification function coefficients of 15 important food items of seasonal diets of coyotes from southeastern Idaho.

	Season			
	Winter	Spring	Summer	Fall
Mammals				
Sylvilagus nuttalli	0.46	0.75	0.69	0.70
Brachylagus idahoensis	0.69	1.18	0.86	0.98
Lepus townsendi	0.55	1.55	0.81	0.86
Microtus montanus	0.56	0.86	0.77	0.79
Thomomys talpoides	0.37	0.63	0.52	0.52
Perognathus sp.	0.20	0.43	0.66	0.39
Cricetid mice	0.48	0.76	0.62	0.88
Antilocapra americana	0.73	1.12	0.79	1.27
Spermophilus townsendi	0.96	1.82	1.11	1.41
Eutamias minimus	0.75	1.25	0.92	1.22
Neotoma cinereus	−0.23	−2.68	−2.21	−2.75
Birds	0.97	1.75	0.99	1.27
Reptiles	0.16	0.41	1.30	0.51
Plant fragments	8.61	9.96	3.90	9.38
Grass macrofragments	0.82	1.09	0.86	0.99
Constant	−21.99	−50.84	−36.17	−42.34

change significantly in relation to other foods consumed and in relation to their availability.

Food items that were indicative of a particular season of feeding by coyotes would generally be expected to exhibit seasonal fluctuations in consumption by coyotes. The relationship of some foods to seasonal use by coyotes, however, was not easily recognized. Grass in winter diets and whitetail jackrabbits in spring diets may represent mathematical relationships important in discriminant function analysis. Nuttall cottontail, pygmy rabbit, montane vole, and most other small mammals occurred in coyote feces in relation to expected seasonal population changes of these prey items. Insects (Coleoptera, Hymenoptera) were consumed in significantly higher proportions by coyotes on the INEL site during winter, when insect populations are low and dormant. Insects insure overwinter survival by burrowing into soil, ground litter, and other substrates. Turkowski (1980) reported a relatively high occurrence of insects in winter scats of coyotes and concluded that coyotes dig beneath the snow and into soil to obtain food.

The seasonal abundance of certain foods in coyote feces supports the idea that coyotes are opportunistic feeders (Meinzer et al. 1975). Nevertheless, the fact that leporids accounted for ½ to ⅔ of coyote diets on the INEL site suggests selectivity. Jackrabbit (*Lepus* spp.) densities were relatively low during this study, and Nuttall cottontails were the most abundant leporid (MacCracken and Hansen 1982). When montane voles and northern pocket gophers are also considered, these food items account for 61 to 87 percent of coyote diets. Johnson and Hansen (1979a) and MacCracken (1980) both reported the occurrence of over 40 items in coyote feces from the INEL site. The fact that 15 percent of all available foods contribute to over 80 percent of food ingested by coyotes supports the contention that coyotes prefer a relatively few mammalian species as food on the INEL site.

ACKNOWLEDGMENTS

The authors thank O. D. Markham, W. J. Arthur, M. K. Johnson, G. C. Lucich, R. L. Potter, E. R. Johnson, and D. Simonson for their participation in this study. This project was supported in part through Grant DE-AS07-76ID01526, MOD 008 from the U.S. Department of Energy, Idaho National Engineering Laboratory Site Ecology Program to Colorado State University.

LITERATURE CITED

ANDERSON, J. E., AND K. E. HOLTE. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. J. Range Manage. 34:25–29.

BAILEY, F. 1907. Destruction of wolves and coyotes. USDA Bur. of Biol. Survey Circ. 63.

BEKOFF, M. 1978. Coyotes: biology, behavior, and management. Academic Press, New York. 383 pp.

CLARK, F. W. 1972. Influence of jackrabbit density on coyote population change. J. Wildlife Manage. 36:343–356.

COOLEY, W. W., AND P. R. LOHNES. 1971. Multivariate data analysis. John Wiley and Sons, New York. 364 pp.

EGGLER, W. A. 1941. Primary succession on volcanic deposits in southern Idaho. Ecol. Monog. 11:277–298.

GIER, H. T. 1968. Coyotes in Kansas. Kansas Agric. Expt. Sta. Bull. 393. 118 pp.

HARNISS, R. O., AND N. E. WEST. 1973. Vegetation patterns of the National Reactor Testing Station, southeastern Idaho. Northwest Sci. 47:30–43.

HOPE, K. 1968. Methods of multivariate analysis. Univ. of London Press. 165 pp.

JOHNSON, M. K., AND R. M. HANSEN. 1979a. Coyote food habits on the Idaho National Engineering Laboratory. J. Wildlife Manage. 43:951–955.

———. 1979b. Estimating coyote food intake from undigested residues in scats. Amer. Midland Nat. 102:363–367.

KLECKA, W. R. 1975. Discriminant analysis. Pages 434–462 *in* W. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds., Statistical package for the social sciences. 2d ed. McGraw-Hill, New York. 675 pp.

LEHNER, P. N. 1976. Coyote behavior: implications for management. Wildl. Soc. Bull. 4:120–126.

MACCRACKEN, J. G. 1980. Feeding ecology of coyotes on the Upper Snake River Plain, Idaho. Unpublished thesis. Colorado State Univ. Fort Collins, Colorado. 85 pp.

———. 1981. Coyote foods in southwestern Colorado. Southwest. Nat. 26:317–318.

MACCRACKEN, J. G., AND R. M. HANSEN. 1982. Herbaceous vegetation of habitat used by blacktail jackrabbits and nuttall cottontails in southeastern Idaho. Amer. Midland Nat. 107:180–184.

MEINZER, W. P., D. N. UECKERT, AND J. T. FLINDERS. 1975. Food niche of coyotes in the rolling plains of Texas. J. Range Manage. 28:22–27.

MURIE, O. J. 1935. Food habits of the coyote in Jackson Hole, Wyoming. USDA Circ. 362. 24 pp.

———. 1945. Notes on coyote food habits in Montana and British Columbia. J. Mammal. 26:33–40.

Sperry, C. C. 1941. Food habits of the coyote. USDI Fish and Wildl. Serv. Res. Bull. 4. 69 pp.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Iowa State Univ. Press, Ames, Iowa. 593 pp.

Taylor, R. G., J. P. Workman, and J. E. Bowns. 1979. The economics of sheep predation in southwestern Utah. J. Range Manage. 32:317–321.

Turkowski, F. J. 1980. Carnivora food habits and habitat use in Ponderosa Pine forests. USDA Forest Service Res. Paper RM-215. 9 pp.

STRUCTURE OF ALPINE PLANT COMMUNITIES NEAR KING'S PEAK, UINTA MOUNTAINS, UTAH

George M. Briggs[1] and James A. MacMahon[2]

Abstract.— A study was made at 18 sites with elevations between 3512 and 3768 m in the Uinta Mountains, Utah. Sites were small in extent but typified vegetation patterns found in the Uintas. Standing crop, species composition (based on dry weight), and values for several physical parameters were determined at each site. Simple linear regressions performed between the various biotic and abiotic characters revealed significant relationships between the characteristics of rocks visible at the surface (the number, size, and variation in size) and vegetation cover. This relationship was probably due to the burial of rocks as a region became vegetated. Bray and Curtis ordinations performed on the data indicated that there were several factors which influenced the species composition but that no single factor dictated the vegetational pattern.

The Uinta Mountains of northeastern Utah are the largest east-west trending range in North America. Much of the alpine and subalpine regions of the range are dominated by members of the Cyperaceae (sedges). These sedge-dominated regions may be placed into two categories: wetland areas and upland areas. In a separate paper (Briggs and MacMahon, in preparation) we discuss the structure of some sedge-dominated wetlands in the Uintas. In this paper we discuss the higher plant composition, standing crop, and physical factors at 18 upland sedge-dominated sites within a small region in the vicinity of King's Peak.

Hayward (1952) published a general description of the vegetation of the Uintas. Lewis (1970) studied the Uinta alpine vegetation and described five alpine communities. Lewis felt that exposure, snowpack, and moisture were important in determining the structure of these communities. Several other workers have considered these factors to be important in determining plant community structure in North American alpine regions (Marr 1961, Holway and Ward 1963, Bliss 1963, Webber et al. 1976). Flock (1978) showed that these factors were also important to the distribution of lichens and bryophytes. Alpine areas also show variation on a smaller scale, with distinct vegetation regions on the order of 20 m^2. Some of these changes can be attributed to microtopographical variations (Billings 1979). In this study we describe the plant associations within a small area (< 1 km^2) of the Uintas and topographical and soil factors associated with these areas.

Study Area

The Uinta Mountains are in northeastern Utah at a latitude of 40°45′ N. They trend almost directly east-west for a distance of 80 km (110–111°W). Bedrock throughout most of the alpine portion of the range is a Precambrian quartzite. Because of the inaccessibility of the Uinta alpine zone (i.e., there are no roads), there are few studies of the area. Climatic data from the region are few but probably are similar to those for the Front Range of the Colorado Rockies. Lewis (1970) estimated precipitation to vary between 85 and 125 cm, with approximately three-fourths of this falling as snow.

We studied an area near King's Peak in the central part of the range, at elevations of 3512–3768 m (11,560–12,300 ft) (Fig. 1). Much of this region consists of cliffs, debris slopes, and felsenmeere, but parts contain a well-developed alpine turf. Cryopedogenic processes are operating in the region, as

---

[1] Department of Botany, University of Montana, Missoula, Montana 59812.

[2] Department of Biology and the Ecology Center, Utah State University, Logan, Utah 84322.

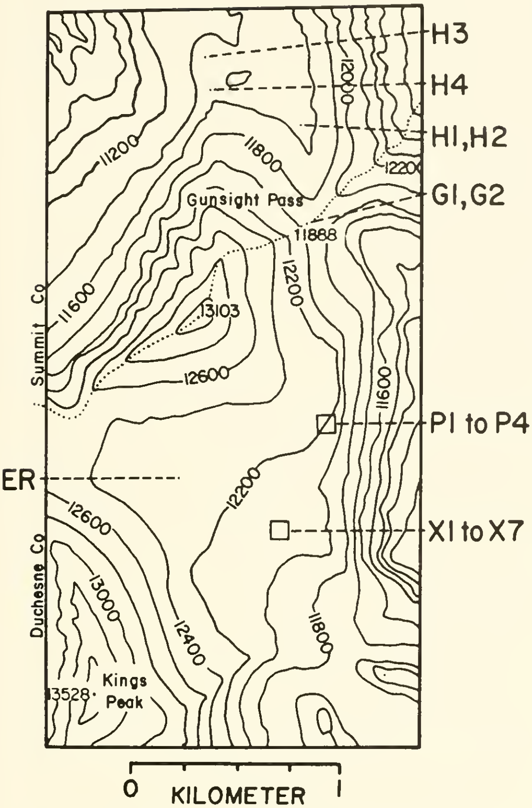


Fig. 1. Map of the vicinity of King's Peak, showing the location of the 18 study sites.

evidenced by stone circles and stripes. Although the vegetated regions often appear homogeneous from a distance, close inspection reveals changes in vegetation, microtopography, and rockiness. The 18 study sites were chosen to illustrate several regions distinguishable to the eye that commonly occur within this small area. These sites are typical of the alpine vegetation of the Uintas in general. It should be emphasized that the size of the study sites was small (30–100 m^2) in comparison to many phytosociological studies but reflected a scale of vegetational change found in the region.

Methods

Nomenclature follows Cronquist et al. (1977) and Holmgren and Reveal (1966) except for *Carex nelsonii* Mkze., which the aforementioned authors have grouped with *Carex nova* L. H. Bailey. We retain *Carex nelsonii* as a separate species based on discussions with Mont Lewis and Arthur Holmgren and on our own observations.

Each alpine site was sampled along a single transect. The boundaries of the area sampled were subjectively set. The initial sample point was randomly chosen; subsequent sample points were regularly spaced. At each sampling point a 20 × 50 cm frame was put down and all the vascular plant material within the frame was clipped at ground level. If possible, the clipped plants were immediately sorted to species and placed in paper bags. Most samples could not be sorted in situ because of the wind. Samples not sorted in the field were placed in paper bags and sorted in the lab. After sorting, all samples were air dried for at least two months and then placed in a drying oven (40 C) for 24 hours and then weighed. Ten samples were collected from each alpine site. Field notes were taken as to the contents of each bag collected. The vegetative identification of *Carex* spp. was not as formidable as might be expected. There were only five species found on the sites (only three were common), rarely did more than two species occur in a single sample bag, and both *Carex paysonis* Clokey and *C. rupestris* All. are quite distinct vegetatively.

One problem facing investigators in both Colorado and Utah is the separation of *Carex elynoides* Holm. and *Kobresia bellardii* (All.) Degland. These species are vegetatively very similar, occupy the same habitat, and fruit infrequently. Separation is easy if fruiting material is present. In all samples having vegetation of the *Carex elynoides-Kobresia bellardii* type each individual fruiting stalk was carefully examined (there were from 0–25 fruiting heads/sample). All the heads examined were *Kobresia bellardii*, and, therefore, all the vegetation of the *Kobresia-C. elynoides* type was considered to be *Kobresia bellardii*.

At each site elevation, slope and aspect were measured. Soil samples were dug on 15 September 1975. Soils were sampled at a depth of 5–10 cm, a depth approximating the middle of the rooting zone. Values for nitrate nitrogen, available phosphorus, and cation exchange capacity were determined by the Utah State University Soil and Water Analysis Laboratory. Gravimetric percent water was determined by weighing soil samples before and after drying (percent = fresh weight–dry weight/dry weight). The pH was determined using a pH meter. A textural analysis was performed by shaking the soils in a series of sieves for five minutes. The percentage of soil, by weight, found in each of the sieves was recorded. A parameter for soil texture was calculated for the samples by giving each size class a weighting factor (1–6) and multiplying the percentage of soil in each size class by the weighting factor, then summing the values for the six size classes. To obtain absolute values for comparison to the relative texture values, the finest and coarsest samples were analyzed by the Utah State University Soil and Water Analysis Laboratory.

The percent cover of soil, rocks, vascular plants, saxicolous lichens, and terricolous lichens was determined by using the line intercept method (Mueller-Dombois and Ellenberg 1974) on three 1 m lines within the sites. The number and average surface area of the rocks encountered in these transects were recorded.

Ordination methods were used to relate the study sites to each other and to elucidate the factors important in structuring the communities. The indirect gradient analysis of Bray and Curtis (1957) was chosen in hope of determining the coenoclines operating in these sedge-dominated regions. A computerized version of the Bray and Curtis method was used. Stands were compared, using the percentage similarity index (PS) where:

$$PS = \frac{2\sum^{i} \min(Pij, Pik)}{\sum^{i} (Pij + Pik)} \times 100$$

Pij = measurement of the ith species in the jth stand.

Pik = measurement of the ith species in the kth stand.

The importance of each species was indexed by its aboveground standing crop (dry weight).

Using the numerical values which depict each site's placement on the ordination axis, simple linear regressions were run relating the vegetational relationships of the sites (as depicted in the values for the ordination axes) to the various measured environmental parameters.

Possible relationships among the various parameters measured at each site were studied through the construction of a correlation matrix that gave correlation coefficients for simple, linear regressions run between each pair of site parameters.

Results and Discussion

The results of the line intercept analysis (Table 1) show the cover percentage in each

Table 1. Standing crop and cover values for the alpine sites.

Site	Standing crop (g/m^2)	Vegetational cover (%)	Soil cover (%)	Rock cover (%)	Soil covered by lichens (%)	Rock covered by lichens (%)
H1	157	99	0	0	–	–
H2	193	99	0	0	–	–
H3	66	66	34	0	9	–
H4	61	73	26	0	–	–
P1	37	20	28	49	31	41
P2	79	67	20	11	10	3
P3	67	61	23	20	20	45
P4	78	56	46	3	49	47
X1	73	79	18	1	7	0
X2	46	37	32	36	0	14
X3	125	91	7	3	0	67
X4	56	24	55	16	0	0
X5	99	63	34	4	43	0
X6	58	39	30	30	13	73
X7	75	35	45	25	47	60
G1	143	72	28	0	11	–
G2	206	99	–	–	–	–
ER	75	–	–	–	–	–

of three categories. Vegetation cover varied from 20 to 99 percent. The amount of surface covered by rocks varied from 0 to 55 percent. The percent of available rock and soil covered by lichens is also shown in Table 1.

The values for the physical parameters measured at each site are given in Table 2. The soil data reflect a lack of soil development. All of the sites were deficient in nitrate nitrogen with values ranging from 0.1 to 3.3 ppm. Phosphorus was also low, ranging from 1.9 to 27 ppm. These values are lower than the 11.2 to 42 ppm values reported by Nimlos and McConnell (1965) for Montana alpine soils. The cation exchange capacity of these soils ranged from 5.3 milliequivalents/100 g soil to 33.3 me/100 g soil. The cation exchange capacity seems high, especially when considering the lack of clay in the soil (see below). The high cation exchange capacity is probably due to the presence of organic matter in the soil resulting from slow decomposition rates.

The texture of all the soils was sandy. Manual sifting gave values of 95 and 100 percent sand. Automated sifting of the two extremes based on our texture scale gave values of 63 and 85 percent sand. These values would define soils classified from sandy loams to loamy sands (Donahue et al. 1971). [The finest soils might be classified a sandy clay if the nonsand fraction (37 percent) were assumed to be more than 18 percent clay. This appears unlikely.] These soils are considerably coarser than most other alpine soils studied. Marr (1961) described soils of the Colorado Front Range which have only 35–59% sand. Nimlos and McConnell's study (1965) of Montana alpine soils describes textures much finer than those of the Uintas. A lack of soil development is expected in any alpine area due to the low temperatures and short growing season. The fact that the Uinta soils are even more poorly developed than other areas of alpine in the western United States is probably due to the quartzite bedrock which weathers slowly and results in a sandy soil that is low in nutrients.

It is obvious that cryopedogenic processes are operating in the Uintas (Lewis 1970). Because these processes result in a size sorting of rocks, it was hoped that values for the following parameters might reflect a particular stage of the cryopedogenic process: mean surface rock size (cm^2); number of rocks visible at the surface; and the normalized variation in surface rock size. Values for these parameters varied at the alpine sites (Table 2). Some of the variation was related to vegetation. It was noted that there appeared to be two extremes in community structure that were related to surface rock characteristics.

TABLE 2. Values for soil parameters, slope, and surface rock characteristics for the alpine sites.

Site	P (ppm)	N (ppm)	CEC (meq/ 100g)	pH	Water (%)	Texture[1]	Slope (%)	Rocks (#)	Rock size (cm^2) ($\bar{x}$)	Rock size ($s/\bar{x}$)
H1	9.6	0.1	11.6	4.9	19	245	8	0	–	–
H2	1.9	0.1	5.3	5.4	9	251	8	0	–	–
H3	5.6	0.3	14.9	5.5	17	252	0	–	–	–
H4	9.1	0.3	12.6	4.2	16	239	30	0	–	–
P1	10.0	3.1	17.4	6.0	20	308	0	85	4.8	1.2
P2	11.0	1.0	17.9	5.6	14	298	12	0.7	9.5	1.1
P3	7.5	1.9	13.5	5.7	20	347	25	36	8.1	0.9
P4	8.4	0.7	14.8	5.5	22	331	4	6	17.4	0.9
X1	13.0	1.7	23.8	5.4	28	320	15	0	241.3	0.9
X2	7.3	3.3	16.2	5.0	26	352	11	30	73.4	2.1
X3	14.0	1.2	32.3	4.8	21	374	5	1	743	0.8
X4	27.0	3.4	20.4	5.1	40	322	8	34	8.0	1.7
X5	9.3	2.4	25.8	5.1	28	366	12	1	584	1.3
X6	8.0	1.0	19.2	4.6	29	348	12	4	142	0.7
X7	3.2	0.3	10.2	4.9	16	334	12	16	35	1.6
G1	13.0	0.7	21.4	6.3	22	374	11	0.3	244	0.7
G2	4.2	0.1	9.8	4.6	10	239	52	0	–	–
ER	0.0	–	–	–	18	–	4	0	–	–

[1] Texture values are on an arbitrary scale. Finer soils have a higher value. See text.

Some areas had a very dense turf with a few large rocks visible at the surface. At the other extreme were areas of sparse vegetation with a large number of rocks of a variable size visible at the surface. This observation is reflected in the correlation coefficients (Table 3), where there were several significant correlations between rock characteristics and standing crop and cover values.

The relationships between surface rock characteristics and vegetation may partially explain some of the correlations between surface rock characteristics and soil parameters. For example, texture was significantly ($p < .05$) related with mean rock size (Table 3). The finest soils were found in areas with large rocks. These were areas with high biomass, where organic matter was added to an otherwise very sandy soil.

There are at least two possible explanations for the significant relationships between surface rock characteristics and vegetation (Table 3). These relationships could reflect a link between cryopedogenesis (that will affect surface rock characteristics) and vegetation, a situation shown by Johnson and Billings (1962). A second possibility is that the relationship between vegetation and surface rock characteristics is due to a simple process of burial of all but the largest rocks as a turf develops. If the surface rock characteristics were reflecting a cryopedogenic process, one would expect a relationship between surface rock characteristics and the percentage of rocks and soil covered by lichens (cryopedogenesis causing instability in rock and soil surfaces and thus a lack of lichens). Because there was no significant relationship between surface rock characteristics and the percentage of lichens on the soil or rocks, we feel that the interaction between vegetation and the surface rock characteristics involves burial.

The peak aboveground biomass varied from 37 to 206 g/m² (Table 1). Lewis' (1970) data on the Uinta alpine zone gave standing crop values ranging from 48.2 g/m² for *Geum*-sedge communities to 83.4 g/m² for *Carex-Kobresia*-grass communities. The Uinta standing crop values are lower than those of other regions of North American alpine tundra. Scott and Billings (1964) reported standing crop values ranging from 14 to 348 g/m² in the Beartooth Mountains of Wyoming; most sites ranged from 100 to 200 g/m². Thilenius (1975) reported an aboveground standing crop value of 223 g/m² in the Medicine Bow Mountains of Wyoming. The low standing crop values in the Uintas may be attributed to the poor soil development. One

Table 3. Correlation matrix for site parameters giving the r value for a simple linear regression between each pair of factors. An asterisk (°) indicates significance at the 0.05 level.

	P	N	CEC	pH	Water %	Texture	Rocks #
P	1	.35	.47	–.14	.62°	.17	–.23
N		1	.22	.25	.58°	.33	.53
CEC			1	–.20	.22	.45	–.32
pH				1	–.22	–.21	.31
Water %					1	.21	–.01
Texture						1	–.19
Rock #							1
Rock size x̄							
s/x̄							
Standing crop							
Vegetational cover							
Soil cover							
Rock cover							
Slope							
Soil covered by lichens %							
Rock covered by lichens %							

possibility is that the sandy texture of these soils allows for little water storage, thereby increasing the chance of drought-stress. Most of the areas we studied had little winter snowpack and were dependent on summer thunderstorms as a source of water. Such thunderstorms are common in the Uintas, but our observations show that the region sometimes goes without rainfall for over a week, in which case the low water-storage capacity of these soils might be important. Data on rainfall and soil water potential would be needed to see if drought is indeed an important factor. Another way in which the poor soil development might affect aboveground standing crop in the Uinta alpine is through low nutrient levels. Our data did not suggest a relationship between nutrient levels and standing crop (Tables 1, 2, and 3), nor did it show that the Uinta alpine was substantially lower in nutrients than some other alpine areas. Our soil sampling was not extensive, and perhaps more sampling of the nutrient levels in these soils would show them to be critical.

Forty-two plant species were sampled on the 18 sites (Table 4). The number of species on any one site varied from 8 to 17. Of the 42 species, 16 were dominants (having 5 percent or more of the aboveground standing crop for a site). The number of dominants at any one site varied from 2 to 5.

Most of the dominant species of the Uinta alpine are dominants of other areas of western alpine regions. *Geum rossii* (R.Br.)Ser. and *Carex rupestris* dominate portions of the Beartooth Range of Wyoming (Scott and Billings 1964) and Niwot Ridge in Colorado (Marr 1961). *Kobresia bellardii* is common on Niwot Ridge but absent in Wyoming. *Carex paysonis* is the only dominant in the Uintas that is not a common dominant in other west ern alpine regions.

The sites we studied fall into three of the communities that Lewis (1970) described: *Carex rupestris* and cushion plant communities, *Geum*-sedge communities, and sedge-grass communities. As Lewis points out, these communities are far from discrete and several of our sites are "transitional" between his basic community types. Moreover, because of the limited size and relative homogeneity of the area we studied, any worker studying the vegetation of the whole range probably would have lumped the entire region into one community: *Geum*-sedge. Close study of this area reveals variation both in vegetation and in several physical factors. In an effort to relate the variation in physical factors with variation in vegetation, and also to better

Table 3 continued.

Rock size x̄	s/x̄	Standing crop	Veg. cover	Soil cover	Rock cover	Slope	Soil with lichens %	Rock with lichens %
.20	.16	.26	.13	.18	−.41	−.36	−.50	−.65°
.03	.55°	.15	−.38	.09	.37	−.47	−.23	−.55°
.89°	−.13	.59°	.54°	−.53°	−.41	−.48	−.30	−.46
−.31	−.29	.14	.12	−.10	−.10	−.45	.20	−.27
.02	.32	−.22	−.33	.45°	.02	−.46°	.23	−.39
.61°	.33	.54°	.17	−.21	−.02	−.20	.16	.46
−.45	.41	−.61°	−.69°	.10	.81°	−.21	−.13	.20
1	−.10	.71°	.60°	−.51	−.42	.01	.01	.50
	1	−.33	−.56°	.34	.52	.05	−.51	−.13
		1	.74°	−.38	−.70°	.56°	.02	−.15
			1	−.66°	−.81°	.56°	−.17	−.10
				1	.12	.02	.11	.69°
					1	−.10	.15	.38
						1	−.21	.17
							1	.62°
								1

compare the different sites, we utilized ordination techniques. Ordination techniques order stands on the basis of their vegetational similarities. Each stand is given a numerical value on one or several axes. The axis values indicate the site's position in a vegetational space (Beals 1973). In the Bray and Curtis ordination, the end stands of the first axis (the x-axis) are the two stands with the lowest percent similarity. All the other stands are arranged relative to the first two. Stands that have a high percent similarity have similar x-axes values. The second axis (the y-axis) is produced by selecting two stands in the center of the x-axis and making them end stands. Again, all stands are arranged relative to these end stands.

Ordinations of all 18 sites were similar if importance values from all species were used or if only the importance values from the dominant species were used. An all-species ordination is illustrated (Fig. 2). ER is clearly separated in the x-axis and H1, H2, H4, and G2 on the y-axis. This separation was expected because these sites were dominated by species not present on other sites: *Carex nelsonii* on ER, and *C. paysonis* on H1, H2, H4, and G2.

Although a significant correlation (r = 0.63) was found between the percent water in the soil and a site's position on the x-axis of these ordinations (Table 5), this correlation is due solely to the site ER. This site was widely separated in the ordination and

Table 4. Species found on the alpine sites. Asterisks (°) indicate that the species constituted greater than 5 percent of the aboveground standing crop.

	H1	H2	H3	H4	P1	P2	P3
Geum rossii (R. Br.) Ser.	°	°	°	—	°	—	—
Carex paysonis Clokey	°	°		°			
Deschampsia cespitosa (L.) Beauv.	°	—		—			—
Polygonum viviparum L.			—	—	—	—	
P. bistortoides Pursh	—	—	—				—
Artemisia scopulorum A. Gray	—			°			
Potentilla spp.	—	—	—	—			
Caltha leptosepala DC.	—			—			
Poa fendleriana (Steud.) Vasey	—						
Festuca ovina L.	—	—	—	—			
Erigeron simplex Greene		—	—	—	—	—	—
Agropyron scribneri Vasey		—					
Trisetum spicatum (L.) Richt.		—					
Poa alpina L.		—					
P. rupicola Nash		—		—	—	—	
Carex rupestris All.			°		°	°	°
Eritrichium nanum (Vill.) Schrad.			—				
Trifolium parryi A. Gray			—		—	—	°
Carex pseudoscirpoidea Rydb.			—				
Hymenoxys grandiflora (Torr. & Gray) Parker			—			—	—
Smelowskia calycina C. A. Meyer							
Draba spp.			—				
Silene acaulis L.			—		—	—	—
Kobresia bellardii (All.) Degland					°	°	—
Arenaria obtusiloba (Rydb.) Fernd.				—	—		—
Paronychia pulvinata A. Gray							—
Danthonia intermedia Vasey							—
Agrostis humilis Vasey							
Salix nivalis Hook.				—			
Castilleja pulchella Rydb.							
Luzula spicata DC.				—			
Carex misandra R. Br.							
C. nelsonii Mkze.							
Lloydia serotina Reichb.							
Eriophorum chamissonis C. A. Meyer							
Antennaria alpina (L.) Gaertn.				°			
Juncus parryi Engelm.				°			

had four times the percent water of any other site (Table 2). Elimination of this site reduced the r to 0.03. In a similar manner a site's position on the y-axis of the 18 site ordinations was significantly associated with texture, cover values, and standing crop. These represented relationships between these parameters and the sites H1, H2, H4, and G2. To see if specific trends for the other sites might become apparent, ordinations were run with 17 sites (eliminating ER) and with 13 sites (eliminating ER and H1–H4). Although there were some significant relationships between site parameters and ordination axis values, these represented separation of end stands from the rest of the sites and not general trends within the data as a whole.

The vegetation of these regions does not appear to be ordered on any of the site parameters we studied, although there do appear to be specific relationships with certain sites (e.g., nearby springs producing sites like ER, slopes producing sites like G2). The variation in the vegetation of the region as a whole is dependent upon the tolerances and capabilities of individual species (Gleason 1939). For example, the distribution of *Kobresia bellardii* is associated with areas of low snow accumulation (Bell and Bliss 1979). In the alpine areas that we studied it appears that a variety of different factors are limiting the distribution of plant species and that no one factor is critical to the distribution of several species as a group.

Table 4 continued.

P4	X1	X2	X3	X4	X5	X6	X7	G1	G2	ER
∘	∘	∘	∘	—	∘	∘	∘	∘	∘	—
									∘	
	—		—	∘			—	—	—	∘
—			∘	∘	—	—	∘	—		—
—	—		—	—						
	—	—	—	∘		—	∘		—	
				—				—	—	
										∘
—		—	—		—	—		—	—	
—	—	—			—	∘	—	—	—	
									—	
					—			—		
∘	∘	∘	∘		—		∘	∘		
	—	—				∘	∘	—	—	
—	—	—	—	—	∘		∘	—		
—								—		
—		—				—		—		
								—		
—		—	—			∘				
∘	∘	—			∘	∘				
						—				
—								—		
	—									
		—	—	∘			—			
		—				—	—			
			—	—		—				
			—	—						—
				∘			—			∘
						—	—			
										—
										—

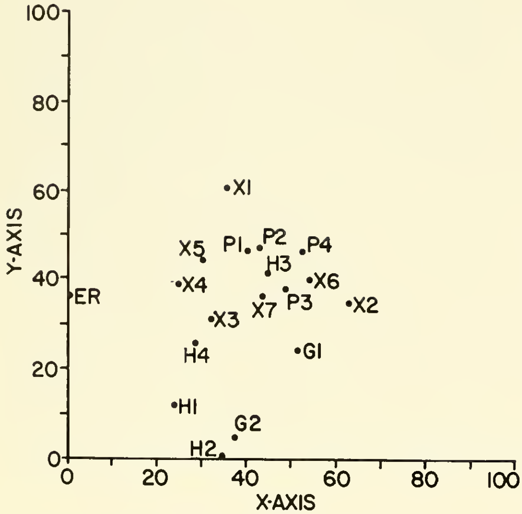


Fig. 2. Ordination of all 18 sites studied, using all species sampled.

Literature Cited

Beals, E. W. 1973. Ordination: mathematical elegance and ecological naïveté. Journal of Ecology 61:23–35.

Bell, K. L., and L. C. Bliss. 1979. Autecology of *Kobresia bellardii*: why winter snow accumulation limits local distribution. Ecological Monographs 49:377–402.

Billings, W. D. 1979. High mountain ecosystems. Evolution, structure, operation, and maintenance. Pages 97–125 *in* P. J. Webber, ed., High altitude geoecology. AAAS Selected Symposium 12.

Bliss, L. C. 1963. Alpine plant communities of the Presidential Range, New Hampshire. Ecology 44:678–697.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Cronquist, A., A. H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. 1977. Intermountain flora: vascular plants of the Intermountain West. Vol. 6. Columbia Univ. Press, New York. 584 pp.

Donahue, R. L., J. C. Shickluna, and L. S. Robertson. 1971. Soils: an introduction to soils and plant growth. Prentice-Hall, Englewood Cliffs, New Jersey.

Flock, J. W. 1978. Lichen-bryophyte distribution along a snow-cover-soil-moisture gradient, Niwot Ridge, Colorado. Arctic and Alpine Research 10:31–45.

Gleason, H. A. 1939. The individualistic concept of the plant association. American Midland Naturalist. 21:92–110.

Hayward, C. L. 1952. Alpine and biotic communities of the Uinta Mountains. Ecological Monographs 22:93–118.

Holmgren, A. H., and J. L. Reveal. 1966. Checklist of the vascular plants of the Intermountain Region. U.S. Forest Service Research Report INT-32. Intermountain Forest and Range Experiment Station, Ogden, Utah. 160 pp.

Holway, J. G., and R. T. Ward. 1963. Snow and meltwater effects in an area of Colorado alpine. American Midland Naturalist 69:189–197.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecological Monographs 32:105–135.

Lewis, M. E. 1970. Alpine rangelands of the Uinta Mountains, Ashley and Wasatch national forests.

Table 5. R values for simple linear regressions ran between ordination axes and site parameters. An asterisk (*) indicates significance at the 0.05 level.

	All 18 sites			
	All species		Important species	
Factor	x	y	x	y
Phosphorus	.37	.29	.26	.01
Nitrogen	.20	.43	.25	.37
Cation exchange	.12	.12	.04	.36
pH	.34	.27	.53*	.36
Water (%)	.63*	.31	.67*	.18
Texture	.39	.51*	.37	.43
Rocks #	.01	.08	.01	.23
Rock size x̄	.45	.28	.32	−.25
Rock s/x̄	.04	.04	.07	−.27
slope	−.18	−.67	.17	.41
Standing crop	.14	−.82*	.11	−.71*
Veg. cover	.38	−.59*	.20	−.49
Soil cover	.16	.56*	.18	.59*
Rock cover	.38	.29	.17	.44
Soil covered by lichen (%)	−.21	−.05	−.26	−.18
Rock covered by lichen (%)	.38	.19	.22	.15

United States Department of Agriculture, Ogden, Utah. 75 pp.

Marr, J. W. 1961. Ecosystems of the east slope of the Colorado Front Range. Univ. of Colorado Studies Series in Biology, No. 8. Univ. of Colorado Press, Boulder, Colorado. 134 pp.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 pp.

Nimlos, T. J., and R. C. McConnell. 1965. Alpine soils of Montana. Soil Science 99:310–321.

Scott, D., and W. D. Billings. 1964. Effects of environmental factors on standing crop and productivity of an alpine tundra. Ecological Monographs 34:243–270.

Thilenius, J. F. 1975. Plant production of three high-elevation ecosystems. Pages 60–75 *in* D. H. Knight, coord., The Medicine Bow ecology project, final report, February 28, 1975. Univ. of Wyoming, Laramie, Wyoming, for Division of Atmosphere and Water Resource Management, Bureau of Reclamation, U.S. Dept. Interior, Denver, Colorado.

Webber, P. J., J. C. Emerick, D. C. Ebert May, and V. Komarkova. 1976. The impact of increased snowfall on alpine vegetation. Pages 201–255 *in* H. W. Steinhoff and J. D. Ives, eds., Ecological impacts of snowpack augmentation in the San Juan Mountains of Colorado. Colorado State Univ. Press, Ft. Collins.

Table 5 continued.

17 sites				13 sites			
All species		Important species		All species		Important species	
x	y	x	y	x	y	x	y
–.14	.14	–.39	.27	–.28	.28	–.76	–.37
.24	–.20	.02	.52°	.01	–.01	–.23	.11
.13	.37	–.02	.42	–.21	–.17	.01	.40
.59°	–.38	.49	.35	–.18	.13	.12	.16
.02	–.16	–.08	.50	–.08	.08	–.60°	–.23
.62°	–.39	.14	.53°	–.10	–.15	.18	.26
.21	.01	.06	–.15	.25	–.15	–.45	.26
–.46	–.07	–.23	–.29	–.17	–.26	.30	.37
.25	.17	–.50	–.01	.19	–.29	–.27	–.20
–.39	.35	.01	.52°	.01	.52°	.13	.55°
–.23	.38	–.23	–.85°	–.48	–.01	.21	.22
–.36	.36	–.14	–.72°	.09	.22	.32	.36
–.18	.08	–.05	–.08	–.05	–.08	.58°	.37
.26	.08	.26	–.21	.26	–.21	.16	.05
.35	–.21	–.35	–.17	.01	–.55°	–.23	.22
–.24	–.49	.07	–.86°	–.23	.28	–.19	.58°

OBSERVATIONS ON THE REPRODUCTION AND EMBRYOLOGY OF THE LAHONTAN TUI CHUB, *GILA BICOLOR*, IN WALKER LAKE, NEVADA

James J. Cooper[1]

Abstract.— Various aspects of the reproduction and embryology of Walker Lake Lahontan tui chub, *Gila bicolor*, were investigated during the spring-summer period of 1976, 1977, and 1981. Tui chub were found to spawn in littoral regions of the lake beginning in late May or early June. Early in the season male chub substantially outnumbered females over the spawning grounds, with a normal 1:1 sex ratio gradually approached as the season progressed. The developmental period between fertilization to hatch-out was shortened by increases in water temperature. Selected stages of embryonic development are described from egg fertilization through post-hatch.

The Lahontan tui chub, *Gila bicolor*, is a cyprinid found in the Columbia, Klamath, and Sacramento river systems as well as in a number of isolated interior basins of California, Oregon, and Nevada (Bailey and Uyeno 1964, Moyle 1976). The Walker, Carson, Truckee, and Humboldt river system of the Lahontan Basin all support populations of tui chub (La Rivers 1962), as well as numerous isolated springs in the north central Great Basin (Hubbs et al. 1974).

Little information exists concerning the reproductive behavior and embryology of the tui chub, especially in the Lahontan system, where they are an integral trophic link in the food chain and heavily preyed upon by various piscivorous fishes. Kucera (1978) reported on the reproductive biology of the tui chub from Pyramid Lake, Nevada. Kimsey (1954) described some early life history information of the tui chub from Eagle Lake, California. Harry (1951), working on the same project produced one of the first papers on tui chub embryology. Spawning and general reproductive behavior of tui chub in East and Paulina lakes, Oregon, was described by Bird (1975). Other less quantitative literature on the subject includes observations on Pyramid Lake, Nevada (Snyder 1918, La Rivers 1962).

Study Area

Walker Lake, the second largest natural body of water entirely within the state is located in west central Nevada approximately 209 km southeast of Reno and 10 km north of Hawthorne. The lake is a remnant of pluvial Lake Lahontan, which once occupied west central and northwestern Nevada as well as the Honey Lake region of northeastern California (La Rivers 1962). Walker Lake is a terminal, alkaline-saline lake with a total dissolved solids content of over 12,500 mg/l, of which sodium chloride, sulfates, and bicarbonates make up approximately 97 percent of the total ionic content (Koch et al. 1979).

Walker Lake has a surface area of 15,000 ha and a maximum length of 25 km and maximum width of 9 km. The maximum depth of the lake is near 33 m and the mean depth is 20 m. The elevation of Walker Lake has been declining very rapidly in recent geological time, with subsequent increases in salinity and alkalinity. Since 1915 the level of the lake has dropped at an average rate of 0.58 m per year (Koch et al. 1979). Upstream agricultural diversion of the Walker River, the only tributary entering the lake, has been the primary factor responsible for the increased rate of desiccation since the turn of the century.

Methods

The data presented in this paper were collected during the spring-summer period of 1976, 1977, and 1981. Observations of tui chub spawning in Walker Lake were accomplished by slowly and quietly approaching shore areas during the spawning season. Spawning chub were easily detected as their fins would break the water surface, their presence many times accompanied by splashing. Sampling techniques included the use of a 15.2 m beach seine, multipaneled gill nets, and hook and line. Notes on behavior and environmental variables such as water temperature, depth of spawning, and substrate type were all recorded concurrently.

---

[1] Bioresources Center, Desert Research Institute, Reno, Nevada 89506.

The embryological development of the tui chub was observed and monitored through an incubation system that closely simulated lake conditions. Two 6.5 l May-Sloan hatching jars were set up at the Desert Research Institute's mobile laboratory on the shore of Walker Lake. Lake water was pumped to a large holding tank on a hill behind the facility and a line was installed to each jar. Each of the lines was equipped with a valve to control flow volumes through the hatching jars at 0.5–1 l per minute. During the incubation periods temperature was monitored at least every four hours with a thermometer measuring to the nearest 0.5 C.

Spawn was obtained by capturing ripe males and females in gill nets set near shore. At least two females and five males were used to produce the fertilized eggs for each incubation period. Ripe females were spawned by hand into a flat-bottomed plastic bowl immediately after capture. Milt from ripe males was extruded over the eggs and lake water added. After the water was added, the bowl was swirled gently to mix the sperm and eggs. After the initial mixing, the fertilized eggs were allowed to stand for a few minutes and then were thoroughly rinsed with lake water a number of times. Approximately one-half hour after water hardening, the eggs were introduced to the hatching jars.

Developmental sequences were obtained with the use of a compound Tiyoda microscope and a 35 mm Minolta camera with a Vivitar microscope adaptor, using Kodak-Kodacolor ASA 125 film. It was found that micrograph magnification revealed the most detail at 40X. Line drawings were produced from these photographs.

Results and Discussion

Spawning

Tui chub from Walker Lake became sexually mature during the spring of their third year, with the exception of a few males that were observed to be mature at the end of the second year. This age is consistent with what Kimsey (1954) found in Eagle Lake, California, and Kucera (1978) in Pyramid Lake, Nevada.

Male and female tui chub are easily identified to their sex during the spawning season. The most obvious change occurs in the male who become covered with small nuptial tubercles. The females undergo a slight enlargement of the anal region and exhibit a marked protrusion of the genital papilla. In both sexes the fins take on a slight reddish coloration.

Spawning activity was first observed on 8 June and 20 May in 1976 and 1977, respectively, at Walker Lake. The surface water temperature on 8 June was 16.5 C and on 20 May was 13.5 C. Kimsey (1954) found spawning to first occur in Eagle Lake near a temperature of 15.5 C.

Spawning observations revealed large schools of chub within 1–2 m of the shoreline at a depth of from .25 to 1 m. The dorsal and caudal fins of the fish broke the surface of the water in many instances. Substrate type varied from small pebbles to large rocks with small amounts of algae attached to their surface in many cases. Actual spawning was not observed, but an examination of a spawning site revealed a number of chub eggs between the rocks and attached to algae.

Available literature is consistent in stating that tui chub are inshore spawners. In Eagle Lake, California, mature tui chub were found to migrate from the deeper southern end of the lake to the shallower northern end during the spawning season (Kimsey 1954). La Rivers (1962) also made the observation that tui chub congregate in shallow shoreline areas to spawn. Gill net catches at Pyramid Lake revealed that 97 percent of the adult benthic tui chub population was inshore in July (Vigg 1978).

Sex ratios were calculated from a sample of 852 fish collected over a 15 month period.

The ratio of males to females was 1:1.16, which does not deviate substantially from an assumed 1:1 ratio. Pyramid Lake female tui chub were found to survive to an older age than males (Kucera 1978), which may explain the sex ratio favoring females in Walker Lake.

Nevertheless, this ratio deviates dramatically during the spawning season. On 29 May 1981, 103 tui chub were captured by seining schools over their spawning ground. Males outnumbered females 84 to 19, which is a sex ratio or 4.4:1. From this group, age III fish were represented by 81.5 percent of the individuals, with the remainder ages II, IV, and V.

Gill netting from June through July 1976 at inshore locations also revealed males entering spawning grounds earlier than females (Fig. 1). On 15 June males comprised 85.1 percent of the population but decreased to 54.3 percent by 19 July. Kucera (1978) found similar results in Pyramid Lake, where from May to June males increased from 49 to 62 percent.

Also of significance are the apparent sexual differences in readiness to spawn at various times in the season. Early in the spawning season (late May) all the males were "running ripe" with sperm, whereas none of the females would extrude their eggs following gentle pressure to the abdominal region. The peak in spawning activity was estimated to occur in mid-July, when the sex ratio again approached normality and a majority of the females in the catches were in a ripe condition. Ripe female chub were difficult to find in gill net sets in late July and early August, although all the males would continue to discharge sperm with gentle handling. From a

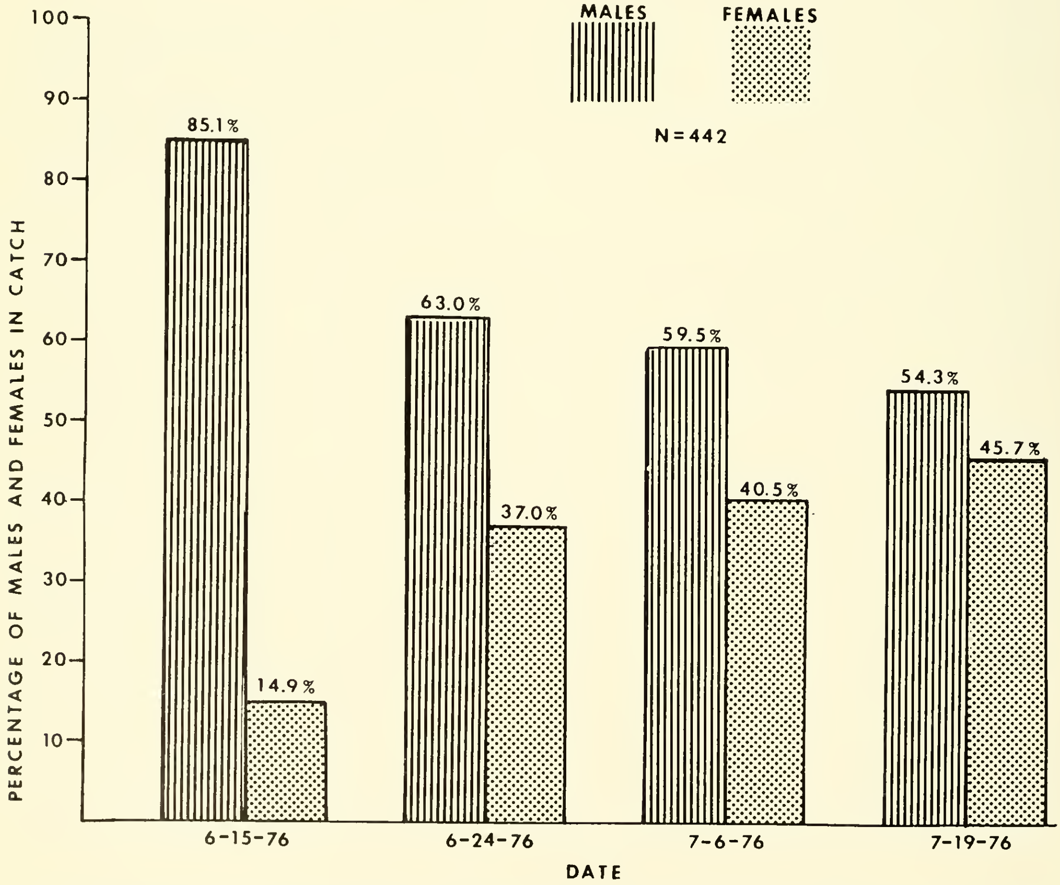


Fig. 1. Percentage of male to female Lahontan tui chub caught in bottom set gill nets in from 5 to 7 m of water between 15 June and 19 July 1976 in Walker Lake, Nevada.

total of 174 females collected from an inshore gill net set, only 3 individuals (1.7 percent) were in a running ripe condition on 4 August. Upon examination of apparently spent females, it was found that they still contained eggs, a fact that suggests multiple and protracted spawning.

It appears as though males are the first to become sexually active in the spring and the last to become inactive at the termination of the spawning season. Reproductive behavior such as this would seem to ensure many spawning males for each female and in turn a greater chance of egg fertilization.

Embryonic Development

Observations on the embryological development and early larval stages of the tui chub were conducted from mid-July to early August 1976 on Walker Lake. The rate of development was found to be dependent upon water temperatures (Fig. 2). An increase in temperature from 18.8 to 24.4 C accelerated embryo development by approximately 85 percent.

Harry (1951) incubated tui chub eggs from Eagle Lake, California, at 7.2 C for the first 100 hours and then allowed temperatures to vary from 1.1 to 28.9 C. At this variable temperature regime the eggs hatched out on the 12th day of incubation. Kimsey (1954) also incubated Eagle Lake tui chub eggs in a quart jar, where the air temperature fluctuated from 4.4 to 32.2 C, and found the fry actively feeding in 9 days. In East Lake, Oregon, Bird (1975) hatched out tui chub eggs in 192 and 142 hours at 14.6 and 21.9 C, respectively. He concluded that highly fluctuating incubation temperatures retarded the developmental period in comparison to stable temperature regimes.

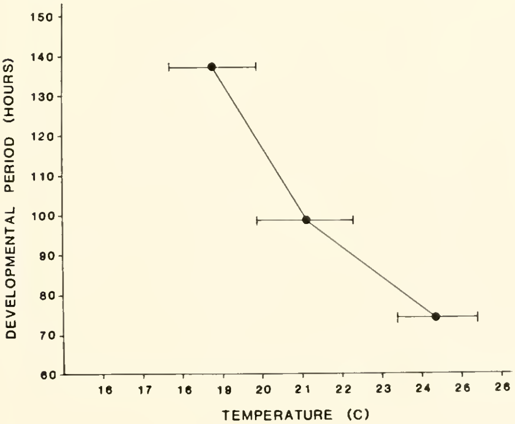


Fig. 2. Developmental period for Lahontan tui chub eggs incubated at three mean water temperatures, July and August 1976, Walker Lake, Nevada. Bar equals two standard deviations.

The ability of tui chub eggs to tolerate wide variations in water temperatures is a valuable survival trait for the species. The eggs incubate in water that is shallow enough to warm up during periods of high solar radiation and cool down at night. The short duration of the egg stage is also a highly beneficial adaptation because environmental conditions have a shorter period of time to cause mortality at this critical stage of development.

Lahontan tui chub eggs flow freely from females when they are in a condition to accept fertilization. It was found that when eggs were forcibly extruded fertilization would not occur. Freshly stripped eggs are approximately 1–1.5 mm in diameter, yellowish, opaque, and very adhesive. They are demersal and their specific gravity is considerably more than that of Walker Lake water because the eggs quickly sink to the bottom. After successful fertilization, the perivitelline space becomes separated from the zygote and swelling occurs, giving the egg as a whole an outer diameter of 1.5–1.8 mm.

Stages of embryonic development were monitored continuously from fertilization through hatch-out (Fig. 3). At 21.1 C, by 6 hours the blastodermal cap had formed at the animal pole and covered about one-fourth of the circumference of the yolk. Mid-gastrulation had occurred by 10 hours and late gastrulation by 12.5 hours, with the embryo becoming recognizable around the yolk. After 22.5 hours of incubation, the embryo length was approximately two-thirds of the way around the yolk circumference, with the head region discernible from the tail. At 31 hours the embryo had 6–8 somites, the optic vesicles were easily discernible, and the yolk sac was still very large. The embryo began to squirm within the egg case at 44.5 hours and the notochord was visible. At this stage the heart, as well as blood flowing throughout the circulatory system, could be seen. Just prior to hatching at 96 hours, the embryo had surrounded the egg yolk and completely filled the chorion. At this stage the eyes had become pigmented, and the embryo moved almost constantly. Just after hatching, the larva body is curved with slight pigmentation, the swim bladder is visible, and they tend to swim periodically. Afterwards they quickly sink to the bottom. This is consistent with what Bird (1975) found in East and Paulina lakes, Oregon, although Harry (1951) found larvae exceptionally active and able to swim rapidly just following hatching.

By 166 hours after fertilization (70 hours after hatching), the larvae were 8–10 mm long and the pectoral fins had begun to form. Four gill chambers and arches were easily discernible posterior to the eyes, and melanophores covered more than half of the body. Swimming action had increased but had not yet become consistent. The yolk sac was very small at this stage, but feeding had not yet been observed.

The majority of the larvae had died by 237.5 hours, probably of starvation. Most of the fins were present and the body and head were heavily covered with melanophores. Myomeres were well developed and the larva was able to hold itself in a swimming, midwater position. It is presumed that the fish must soon begin to feed at this stage of development because the yolk sac had been completely absorbed.

Literature Cited

Bailey, R. M., and T. Uyeno. 1964. Nomenclature of the tui chub, cyprinid fishes from western United States. Copeia 1964(1): 238–239.

Bird, F. H. 1975. Biology of the blue and tui chubs in East and Paulina lakes, Oregon. Unpublished thesis. Oregon State Univ., Corvallis. 165 pp.

Harry, R. R. 1951. The embryonic and early larval stages of the tui chub, *Siphateles bicolor* (Girard), from Eagle Lake, California. California Fish and Game 37(2):129–132.

Hubbs, C. L., R. R. Miller, and L. C. Hubbs. 1974. Hydrographic history and relict fishes of the north central Great Basin. Mem. California Acad. Sci. 7:259.

Kimsey, J. B. 1954. The life history of the tui chub, *Siphateles bicolor* (Girard), from Eagle Lake, California. California Fish and Game 40(4):395–410.

Koch, D. L., J. J. Cooper, E. L. Lider, R. L. Jacobson, and R. J. Spencer. 1979. Investigations of Walker Lake, Nevada: dynamic ecological relationships. Desert Res. Inst., Bioresources Cent. Pub. No. 50010. 191 pp.

Kucera, P. A. 1978. Reproductive biology of the tui chub, *Gila bicolor* in Pyramid Lake, Nevada. Great Basin Nat. 38(2):203–207.

La Rivers, I. 1962. Fishes and fisheries of Nevada. Nevada Fish and Game Comm. 782 pp.

Moyle, P. B. 1976. Inland fishes of California. Univ. of California Press, Berkeley. 405 pp.

Snyder, J. O. 1918. The fishes of the Lahontan system of Nevada and northeastern California. Bull. U.S. Bur. Fish. 35:31–86.

Vigg, S. 1978. Fish ecology. Chapter 8 in W. F. Sigler and J. L. Kennedy, eds. Pyramid Lake Nevada, ecological study final report. W. F. Sigler and Associates, Inc. Reno, Nevada.

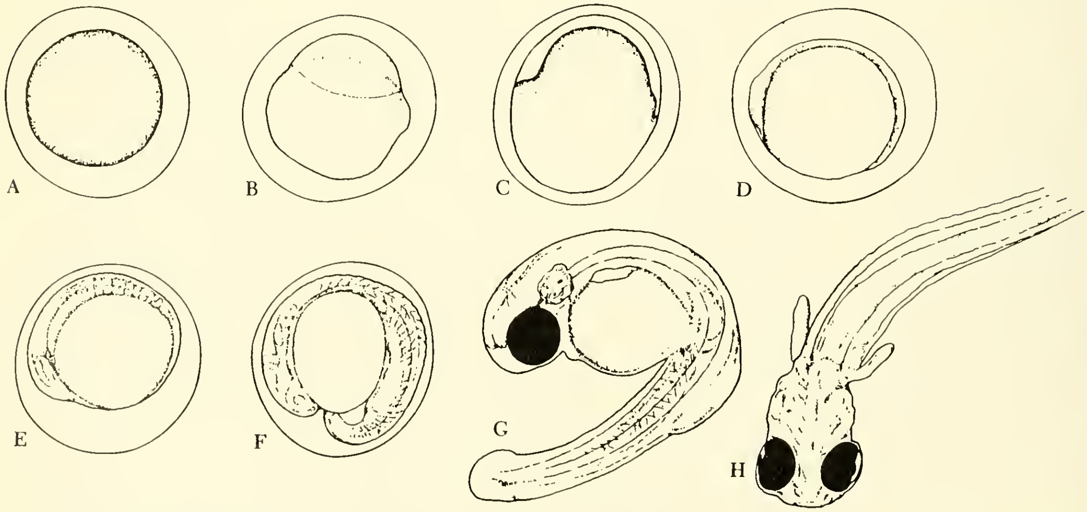


Fig. 3. Developmental sequences of Lahontan tui chub incubated at 21.1 C. A, One hour after fertilization; B, 6 hours; C, 12.5 hours; D, 22.5 hours; E, 31 hours; F, 44.5 hours; G, 96 hours, just after hatching; H, larva 70 hours after hatching.

THE PREVALENCE OF *ECHINOCOCCUS GRANULOSUS* AND OTHER TAENIID CESTODES IN SHEEP DOGS OF CENTRAL UTAH[1]

Lauritz A. Jensen[2], Ferron L. Andersen[2], and Peter M. Schantz[3]

Abstract.— Fifty-one of 62 sheep dogs in central Utah were successfully purged for diagnosis of cestodes in 1981. Tapeworms were identified in the purged fecal samples of 33 (64.7 percent) animals. Minimum infection rates in the dogs which were purged were: 9.8 percent for *Echinococcus granulosus*, 29.4 percent for *Taenia pisiformis*, 27.5 percent for *T. ovis krabbei*, 27.5 percent for *T. hydatigena*, and 2.0 percent for *T. serialis*. The prevalence of *E. granulosus* decreased from 27 percent in 1971 to 9.8 percent in 1981.

Echinococcus granulosus is endemic in dogs in central Utah and is primarily confined to sheep-raising communities (Andersen et al. 1973). The proportion of infected dogs among those brought to voluntary diagnostic clinics has gradually decreased from 27 percent in 1971 (Loveless et al. 1978) to 18 percent in 1978 (Condie et al. 1981). In the past, surveys have included all classifications of domestic dogs (e.g., family pet, guard dog, sheep dog, hunting dog, etc.), regardless of the feeding habits. To help determine the effectiveness of the hydatid disease control program in Utah, and to ascertain if the prevalence of *E. granulosus* is in a continued decline, 62 sheep dogs were tested in Sanpete and Summit counties during August and October 1981.

Field clinics were conducted in the general vicinity of summer range allotments so as to be convenient for sheep herders. Owners were requested to fast their dogs 12 hours prior to the examination. A solution of 1.5 percent arecoline hydrobromide was administered orally (3 mg/kg of body weight) to induce purging, after which the mucoid portion of the purge was diluted in water and examined for tapeworms. Specimens of *E. granulosus* were washed in tap water for 30 minutes and fixed in AFA, whereas the larger taeniids were relaxed in water for 6 hours at ambient temperature and fixed in formalin. Table 1 details the results of the survey.

Fifty-one of 62 dogs, which ranged in age from six months to nine years, were successfully purged. Tapeworms were recovered from the purged fecal specimens of 33 dogs. Infections with *E. granulosus* were identified in 5 of 51 (9.8 percent) dogs, representing four separate sheep herds. Two of the four owners of these herds previously had had hydatid cysts removed from their liver or lung, and had participated in past field clinics. The rates of infection in the 51 dogs were: 29.4 percent for *Taenia pisiformis*, 27.5 percent for *T. ovis krabbei*, 27.5 percent for *T. hydatigena*, and 2.0 percent for *T. serialis*. The total burden of *Taenia* in infected dogs ranged from one to 233, with mixed infections of two or more species of worms being common. There was no obvious relationship between the age of the parasitized dogs and the proportion of dogs infected, and it was not uncommon for pups, approx-

Table 1. Cestodes recovered from 51 sheep dogs of central Utah.

	No. dogs infected		
Cestode	Sanpete Co. (n = 38)	Summit Co. (n = 13)	Total % dogs infected
Echinococcus granulosus	5	0	9.8
Taenia hydatigena	5	9	27.5
Taenia ovis krabbei	12	2	27.5
Taenia pisiformis	12	3	29.4
Taenia serialis	1	0	2.0

---

[1] Supported in part by NIH Grant AI-10588-10

[2] Department of Zoology, Brigham Young University, Provo, Utah 84602.

[3] Parasitic Diseases and Veterinary Public Health Division, Center for Disease Control, Atlanta, Georgia 30333.

imately six months old, to harbor gravid taeniids. Dogs infected with *E. granulosus* were injected with praziquantel (Droncit, Bayvet Division, Cutter Laboratories, Shawnee, Kansas) at a dosage level of 5 mg/kg of body weight.

Comparison of the 9.8 percent rate of infection of *E. granulosus* in 1981 to 27 percent in 1971 (Loveless et al. 1978) and 18 percent in 1978 (Condie et al. 1981) suggests a true reduction. This suggestion is further supported by the fact that only dogs at highest risk, i.e., sheep dogs, were examined in the study herein reported. It is also apparent from the taeniids recovered that sheep herders still feed their dogs ample supplies of sheep viscera, deer, and rabbits. Even though most owners of large sheep herds appear to cooperate and do not give their dogs sheep viscera or wild animals, the transient, hired herders may be less disciplined. Thus, yearly field clinics and educational programs on diseases caused by cestodes should be continued.

Representative specimens: *E. granulosus* USNM Helm. Coll. No. 76786; *T. pisiformis* No. 76787; *T. ovis krabbei* No. 76788; *T. hydatigena* No. 76789; *T. serialis* No. 76790.

LITERATURE CITED

ANDERSEN, F. L., P. D. WRIGHT, AND C. MORTENSON. 1973. Prevalence of *Echinococcus granulosus* infection in dogs and sheep in central Utah. J. Amer. Vet. Med. Assoc. 163:1168–1171.

CONDIE, S. J., J. R. CRELLIN, F. L. ANDERSEN, AND P. M. SCHANTZ. 1981. Participation in a community program to prevent hydatid disease. Publ. Hlth. Lond. 95:28–35.

LOVELESS, R. M., F. L. ANDERSEN, M. J. RAMSAY, AND R. K. HEDELIUS. 1978. *Echinococcus granulosus* in dogs and sheep in central Utah, 1971–1976. Amer. J. Vet. Res. 39:499–502.

GROWTH OF JUVENILE AMERICAN LOBSTERS IN SEMIOPEN AND CLOSED CULTURE SYSTEMS USING FORMULATED DIETS

S. R. Wadley[1], R. A. Heckmann[1], R. C. Infanger[1], and R. W. Mickelsen[1]

Abstract.— Growth of juvenile American lobsters, *Homarus americanus*, raised in four semiopen culture systems, with daily water exchange rates ranging from 29 percent to 3.3 percent, was compared with growth in a completely closed system. Animals were fed a formulated pelleted ration, water quality factors were measured daily, and changes in concentration of nitrate, orthophosphate, and total organic carbon were monitored. Results of two 90-day trials indicate that growth increased in the system with the lower water exchange rates. Maximum growth occurred in the closed system.

Interest in commercial culture of the American lobster, *Homarus americanus*, has increased because of high consumer demand and declining natural fisheries. Dow (1980) indicates that this decline is probably due to overexploitation of the lobster. He states that during the period from 1950 to 1976, inshore landings of lobsters from Newfoundland to New York decreased from 33,000 to 30,000 metric tons and the number of traps used increased from 240,000 to 520,000. Other data indicate that in some areas annual trap success has also declined from 225 pounds per trap in 1889 to 17 pounds per trap in 1970 (John T. Hughes, pers. comm.).

The American lobster is one of four marine species given "high priority" status for aquaculture by the U.S. National Oceanographic and Atmospheric Administration because it meets several requirements for commercial production of aquatic species (Glude 1977). These criteria include adequate consumer demand, high profit potential, ability to complete the life cycle in captivity, high food conversion efficiency, and resistance to disease (Cobb 1976). The economic potential of lobster culture depends on satisfaction of these factors, plus the development of efficient larval rearing and grow-out systems, production of inexpensive diets, and determination and maintenance of optimum culture environments. The last two factors (formulated diets and determination of optimum conditions) are studied in this experiment.

Numerous studies have been done on basic nutritional requirements of crustaceans (Gallagher et al. 1979, Winget et al. 1976, Castell and Covey 1976). Most researchers agree that formulated diets must replace expensive natural rations for lobster culture to be economically feasible (Van Olst et al. 1980). Conklin et al. (1975) define nutritional requirements for lobsters and report initial development of pelleted rations. The formulation of diets in pellet form is desirable in aquaculture because of ease in production, handling, and feeding (Conklin 1980). Goldblatt et al. (1978) and Infanger et al. (1980) indicate that pelleted rations may lose nutritional quality through vitamin leaching when exposed to culture water. This makes most diets developed thus far unacceptable for lobster culture.

Culture systems are usually classified as open, semiopen, or closed. Wheaton (1977) described open systems as production in a natural body of water with few modifications, semiopen systems as those where water is taken from a natural source, passed through the system once and discarded, and closed systems as those where water is placed within the system and is rarely if ever replaced. The economic production of lobsters is restricted to semiopen and closed systems because natural water temperatures in most areas are below optimal growth temperatures and must be heated to accelerate animal growth.

---

[1] Department of Zoology, Brigham Young University, Provo, Utah 84602.

Many factors have been used in comparing semiopen and closed systems for culture of marine organisms (King 1973). One important contrast for lobster culture may be differences in growth rates between systems. It is unknown if juvenile lobsters will grow faster in a particular type of system. The purpose of this experiment was to compare lobster growth in five different culture environments ranging from semiopen systems (with four different water exchange rates) to closed systems. Animals in all systems were fed the same formulated diet.

Materials and Methods

Four semiopen systems and one closed system were established in separate 300:1 tanks. Water was removed from each semiopen system and replaced at different intervals, thereby producing daily water exchange rates of 29 percent in system I, 13 percent in system II, 7.4 percent in system III, and 3.3 percent in system IV. Water in system V remained unchanged during the experiment except for addition of fresh water to compensate for evaporation. A 10 cm thick undergravel filter in each tank provided filtration and a substrate for nitrifying bacteria.

Culture water was synthetic seawater similar to that described by Spotte (1970) for large marine aquaria. It was mixed in 1200 liter quantities for use in the experiment.

Forty-eight juvenile lobsters were tested in each culture system. Cages in each tank isolated animals, which allowed monitoring of the growth rate of each animal throughout the experiment.

Two 90-day trials were conducted (trial 1 and trial 2). Growth was determined by measuring animal length from eye socket to posterior margin of the carapace along the dorsal midline. Growth of animals between trials could not be compared because lobsters for each trial were hatched from two different females. Comparisons were made between systems within each trial.

Test animals were fed a pelleted diet similar to those described by Infanger et al. (1980). The pellets were produced using a Wenger extruder (model X-5), then sealed in plastic bags and stored at –18 C. Lobsters were fed daily in excess of what could be consumed during the 24-hour period. Food remaining from the previous day was removed before feeding a fresh pellet.

Water quality was monitored daily in each trial by testing salinity, pH, temperature, dissolved oxygen, and nitrite. All factors, with the exception of nitrite, were measured directly using the appropriate meter. Nitrite was recorded as percent transmittance, using a Bausch and Lomb Spectronic 20 (Spotte 1970).

Results of water quality measurements were compared with optimum levels described for lobster culture (Van Olst et al. 1980). These optimum levels included a temperature range between 20.0 and 22.0 C, 30.0 ppt salinity, 6.4 mg/l dissolved oxygen, a pH of 8.0, and nitrite levels less than 10.0 mg/l. Spotte (1973) recommends nitrite levels less than 0.1 mg/l for large marine aquariums. Because nitrite is a potentially toxic waste compound, the lower concentration of 0.1 mg/l or less was considered optimum. It was determined through use of a standard nitrite solution that a transmittance of 74 percent or higher indicated concentrations lower than this level.

Additional tests were performed on water taken from the first` trial by the certified Brigham Young University Environmental Analysis Laboratory. Samples were tested for two elements (copper and iron) and for three compounds (nitrate, orthophosphate, and total organic carbon). These substances may be important toxins or nutrients in culture systems that may strongly affect animal growth (Spotte 1979, Wheaton 1977). Two samples were tested: one sample was freshly made seawater, and the second was the same water taken from system V after the 90-day culture period.

Three compounds tested in the first trial (nitrate, orthophosphate, and total organic carbon) were tested more extensively in the second trial from all five water systems. Samples were taken at the beginning of the culture period and again prior to a water change in that particular system. For example, an initial sample was taken on day 1 from each system and again on day 4 from system I, on day 7 from system II, on day 14 from system III, and on day 30 from system IV. This testing was duplicated twice from each semiopen system (series A and B). Water samples from system V were taken for analysis on days 1, 30, 60, and 90.

RESULTS

Results of juvenile lobster growth experiments from both trials include: (1) water quality, (2) detailed water analysis, and (3) growth and survival.

Water Quality

Water quality was monitored by daily measurement of temperature, salinity, pH, and nitrite. Temperature averaged 20.0 and 21.0 C, mean salinity was 31.0 and 32.0 ppt, pH averaged 8.1, and mean nitrite transmittance was 91.5 and 94.3 percent in trial 1 and trial 2 respectively.

Dissolved oxygen in trial 1 had a mean concentration of 5.5 mg/l. This value remained constant throughout the trial and represents the saturation level at ambient salinity, temperature, and atmospheric pressure. Dissolved oxygen was not tested in trial 2.

Detailed Water Analysis

In comparing 90-day-old water with freshly made synthetic water in trial 1, levels of iron decreased, whereas concentrations of copper, nitrate, orthophosphate, and total organic carbon increased (Table 1). The last three compounds were tested more extensively in trial 2 and compared with concentrations in all five culture systems.

TABLE 1. Water comparisons: Trial I.

Tests		New[a]	Old[b]	Normal levels
Copper as Cu	(ug/l)	36	49	60[c]
Iron as Fe	(ug/l)	92	66	300[c]
Nitrate as N	(mg/l)	0.46	2.15	20[c]
Phos-Ortho as P	(mg/l)	0.23	2.07	1.0 (ug/l)[d]
Total organic carbon	(mg/l)	16.66	19.60	6.0[d]

[a] Freshly made synthetic seawater
[b] Synthetic seawater after 90 days
[c] From Van Olst et al. (1980)
[d] From Spotte (1979) for marine aquaria

Nitrate

Nitrate concentrations increased with the age of culture water within each of the five systems (Fig. 1). Initial levels were below 1.0 mg/l with the exception of a sample from system I that started at 1.3 mg/l. Final levels ranged from 0.4 mg/l in system I after 4 days to 11.2 mg/l in system V after 90 days. The second set of duplicate tests (series B) showed greater increases of nitrate than the first set of tests (series A) in each semiopen system. This probably occurred because samples for the second series were taken later in the culture period, when biological filters were more efficient in converting ammonia to nitrate.

Nitrate concentration increased inversely with the amount of water replacement in the four semiopen systems. Final concentrations from the second duplicate series were 1.4 mg/l in system I after 4 days, 1.9 mg/l in system II after 7 days, 5.5 mg/l in system III after 14 days, and 10.5 mg/l in system IV after 30 days.

Results from system V showed nitrate increases over the 90-day culture period, when concentration increased from 0.46 mg/l on day 1 to 11.2 mg/l by day 90.

Orthophosphate

Orthophosphate increased with the age of water within each system (Fig. 2). Initial levels ranged from 0.23 mg/l to 0.41 mg/l, whereas final concentrations ranged between 0.67 mg/l in system I to 3.40 mg/l in system

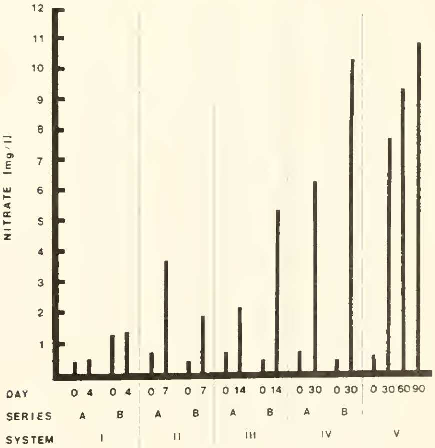


Fig. 1. Nitrate concentration comparisons for systems from trial 2.

V. These levels are greater than concentrations found in natural seawater, but compare favorably with concentrations reported in large marine aquaria (Spotte 1979).

Total Organic Carbon

Levels of total organic carbon (TOC) increased with the age of water within each system (Fig. 3). This increase can be seen in system V, which started at 16.7 mg/l on day 1 and increased to 21.9 mg/l by day 30, to 27.8 mg/l by day 60, and to 28.7 mg/l by day 90.

TOC concentration increases did not correlate with water exchange when systems were compared with each other. The greatest differences occurred in system III, which increased from 14.7 mg/l to 37.5 mg/l in 14 days. The highest final concentration (24.1 mg/l) occurred in system I after only four days.

Growth and Survival

Results indicate that culture systems do affect juvenile lobster growth. In both trials, animals in system V had faster growth rates than any other system (Fig. 4). They were significantly larger ($p = .05$) than in systems I, II, and III in trial 1 and systems I and II in trial 2 (standard Students t-test). Growth in both trials, with the exception of system II in trial 2, have an inverse relationship with daily water exchange rates even though all differences were not significant.

Survival ranged from 46.0 percent to 73.0 percent, averaging 57.2 percent in trial 1, and from 50.0 percent to 90.0 percent, averaging 72.2 percent in trial 2 (Fig. 5). No clear patterns resulted from either trial. System III had the best survival in trial 2 and the most deaths in trial 1.

Discussion

Results indicate that water exchange affected juvenile lobster growth rates when water quality factors (temperature, salinity, pH, dissolved oxygen, and nitrate) were maintained within limits suggested by Van Olst et al. (1980) for lobster culture and by Spotte (1973) for marine aquaria. Growth rates increased in both trials with decreasing water exchange, with the best growth occurring in the closed systems. Reasons for this are unclear, but differences may be partially explained by changes in water chemistry.

Wheaton (1977) indicates that water chemistry will change in culture environments depending on the length of time water remains in the system. Sources of the three compounds tested in trial 2 (nitrate, orthophosphate, and total organic carbon) include leached nutrients from unstable diets and waste products from animal metabolism. Copper and iron were not tested in trial 2 because concentrations did not change greatly in trial 1.

Increase of nitrate in closed systems is well documented (Liao and Mayo 1972, King

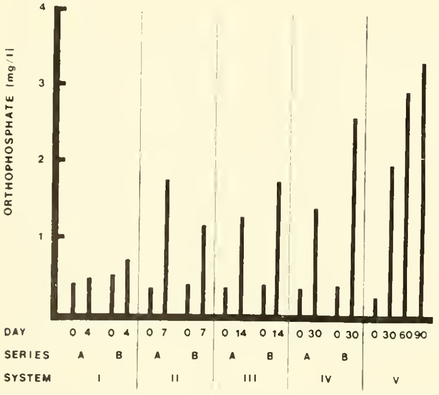


Fig. 2. Orthophosphate concentration comparisons for systems from trial 2.

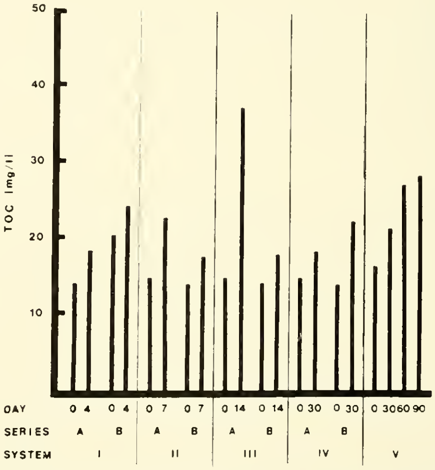


Fig. 3. Total organic carbon concentration comparisons for systems from trial 2.

1973). Toxicity levels of nitrate are unknown for most species, but Van Olst et al. (1980) suggests 500 mg/l as the maximum concentration desirable for lobster culture. Data from this experiment show increases of nitrate relative to the age of the water. Levels of nitrate for all systems (highest concentration was 11.2 mg/l in system V) were well below 500 mg/l, which probably indicates that nitrate was not an important factor in this experiment. Nitrate may become toxic, however, in closed systems designed for very long periods between water changes.

Wheaton (1977) states that most soluble phosphate in aquatic systems is in the form of inorganic orthophosphate. It is excreted by culture animals and also results from autolysis and subsequent mineralization of damaged or dead cells by heterotrophic bacteria (Spotte 1979). Goldblatt et al. (1978) also found small amounts leaching from gluten-based diets similar to the ration used in this experiment. Orthophosphate is removed from aquatic systems by marine algae and by air stripping when the compound is absorbed onto the surface of air bubbles that rise to the surface. Results indicate that concentrations do increase in closed systems. Spotte (1979) states, however, that levels eventually reach equilibrium because of air stripping. Toxic concentrations have not been reported for lobster culture, but increased levels will stimulate algae growth in marine systems (Wheaton 1977). This algae may act as a dietary supplement for culture animals and may account for some of the increased growth in systems with low water exchange.

Organic carbon results from animal wastes and extracellular products of aquatic plants (Spotte 1979). TOC levels may also include water soluble nutrients (vitamins, carbohydrates, and proteins) that leach from unstable pelleted rations. TOC, like orthophosphate, is removed from water systems by air stripping (Spotte 1979). This may account for the random concentrations occurring between systems. No toxic levels have been reported for lobster culture.

All TOC levels reported were at least three times higher than those reported in large marine aquaria (Spotte 1979). This discrepancy occurred because of a difference in analysis procedure. Spotte used wet oxidation, whereas samples from this experiment were analyzed using dry combustion. Williams (1975) reported three- to fourfold differences between these two techniques testing the same water sample.

Mortality in most systems of both trials was very high. This was probably not a result of the water system, but occurred because of low nutritional value of the diet. High mortality has been an inherent problem in lobster culture with the use of formulated diets (Conklin 1980). Recently, rations have been developed that consistently reduce mortalities to less than 10 percent (Rex Infanger and Roger Mickelsen, unpubl. data). This is a significant advancement because low

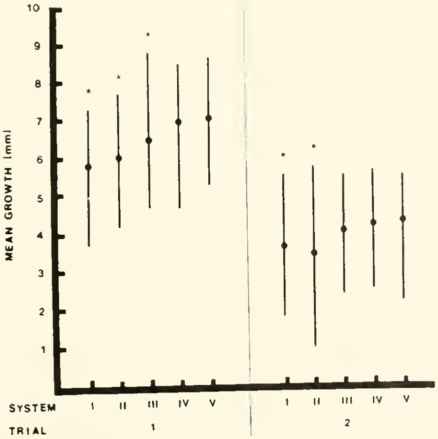


Fig. 4. Means and ranges of growth for trials 1 and 2. ° indicates significantly less growth compared with system V, using the standard Student t-test (p = .05).

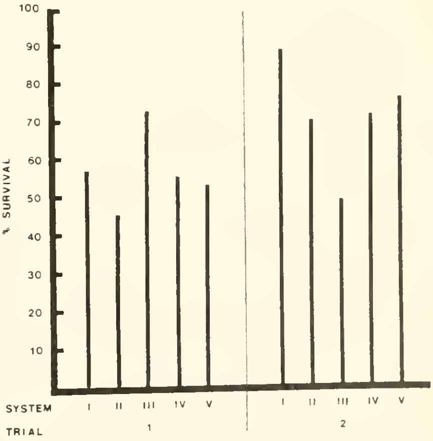


Fig. 5. Survival of juvenile lobsters from trials 1 and 2 after 90 days.

mortality and accelerated growth are necessary for lobster culture to be feasible.

Closed systems provide many advantages over semiopen systems, including lower energy costs in heating and maintaining water temperature, greater efficiency in maintaining ideal culture conditions (salinity, pH, and dissolved oxygen), and fewer disease problems (King 1973). It can be concluded from this experiment that the closed systems tested also produce better growth of juvenile lobsters.

LITERATURE CITED

CASTELL, J. D., AND J. F. COVEY. 1976. Dietary lipid requirements of adult lobsters, *Homarus americanus* (M.E.). J. Nutrition 106:1159-1165.

COBB, J. S. 1976. The American lobster: the biology of *Homarus americanus*. Univ. of Rhode Island Sea Grant Marine Tech. Rep. No. 49. 32 pp.

CONKLIN, D. E. 1980. Nutrition. Pages 277-300 *in* J. S. Cobb and B. F. Phillips, eds., The biology and management of lobsters. Academic Press, New York. Vol. 2.

CONKLIN, D. E., K. DEVERS, AND R. A. SHLEASER. 1975. Initial develpment of artificial diets for the lobster, *Homarus americanus*. Proc. World Mari. Soc. 6:237-248.

DOW, R. L. 1980. The clawed lobster fisheries. Pages 265-316 *in* J. S. Cobb and B. F. Phillips, eds., The biology and management of lobsters. Academic Press, New York. Vol. 2.

GALLAGHER, M. L., R. C. BAYER, D. F. LEAVITT, AND J. H. RITTENBURG. 1979. Formulation of artificial diets for feeding lobster (*Homarus americanus*) held in pounds. Maine Sea Grant Tech. Rep. No. 46.

GLUDE, J. B. 1977. NOAA aquaculture plan. U.S. National Oceanographic and Atmospheric Administration, Washington D.C.

GOLDBLATT, M. J., D. E. CONKLIN, AND W. D. BROWN. 1978. Nutrient leaching from pelleted rations. Pages 117-129 *in* J. E. Halver and K. Tiews, eds., Finfish nutrition and finfeed technology. Heenemann Verlags-gesellschaft, Berlin. Vol. 2.

INFANGER, R. C., R. W. MICKELSEN, R. HECKMANN, AND S. R. WADLEY. 1980. Vitamin leaching in lobster rations. Pages 3-10 *in* R. C. Bayer and A. D'Agostino, eds., Proc. Lobster Nutrition Workshop, Maine Sea Grant Tech. Rep. No. 58.

KING, J. M. 1973. Recirculating system culture methods for marine organisms. SEA Scope 3:2,6-8.

LIAO, P. B. AND R. D. MAYO. 1972. Salmonid hatchery water reuse systems. Aquaculture 1:317-335.

SPOTTE, S. 1970. Fish and invertebrate culture, water management in closed systems. John Wiley and Sons, New York. 145 pp.

———. 1973. Marine aquarium keeping. John Wiley and Sons, New York. 171 pp.

———. 1979. Sea water aquariums. John Wiley and Sons, New York. 413 pp.

VAN OLST, J. C., J. M. CARLBERG, AND J. T. HUGHES. 1980. Aquaculture. Pages 333-384 *in* J. S. Cobb and B. F. Phillips, eds., The biology and management of lobsters. Academic Press, New York. Vol. 2.

WHEATON, F. W. 1977. Aquacultural engineering. John Wiley and Sons, New York. 708 pp.

WILLIAMS, P. J. 1975. Biological and chemical aspects of dissolved organic material in sea water. Pages 301-363 *in* J. P. Riley and G. Skirrow, eds., Chemical oceanography. Academic Press, London. Vol. 2.

WINGET, R. R., R. E. EPIFANIO, T. RUNNELS, AND P. AUSTIN. 1976. Effects of diet and temperature on growth and mortality of the blue crab, *Callinectes sapidus*, maintained in a recirculating system. Proc. Natl. Shellfish Assoc. Vol. 66. 5 pp.

DIAMETER-WEIGHT RELATIONSHIPS FOR JUNIPER FROM WET AND DRY SITES

T. Weaver[1] and R. Lund[2]

Abstract.— Height-diameter (basal or canopy) relationships for *Juniperus scopulorum* trees taken from wet and dry sites were quite different, but total aboveground weight-diameter relationships for trees taken from the two sites did not differ. It is shown that log total weight (kg) = approximately 1.7 + 2.26 log basal diameter (cm) = - 2.55 + 2.98 log canopy diameter (cm). Though the first relationship ($r^2 = 0.98$) is stronger than the second ($r^2 = 0.80$), the canopy diameter-weight relationship may be useful for estimating tree weights from aerial photos. Root-shoot ratios for wet site trees 5, 12, and 31 cm in basal diameter were 37, 27, and 26 percent, respectively.

Linear dimensions are often well correlated with plant biomass (e.g., Kira and Shidei 1967, Weaver and Forcella 1977) and are therefore useful in estimating plant biomass. Basal diameter-weight relationships for many Rocky Mountain trees (Brown 1976, Weaver and Forcella 1977) and shrubs (Brown 1976) have been developed. Crown diameter-weight relationships for several Rocky Mountain shrubs are presented by Weaver (1977); this dimension may be especially useful for low-multistemmed shrubs or for trees seen in aerial photographs.

Because diameter-weight relationships are especially useful if they are general, it is desirable to test for generality by comparing diameter-biomass relationships of individuals of one species from different habitats and exhibiting different life forms. *Juniperus scopulorum* Sarg. is a good test species because (1) it occupies both wet and dry sites, (2) it has a shorter and fuller form on dry than on wet sites, and (3) regression lines should be useful to managers throughout the Rocky Mountain area occupied by the tree (Little 1971).

Methods

Thirteen juniper trees were felled in October 1980. They stood immediately east of the Headwaters of the Missouri State Park, Gallatin County, Montana. Seven of these trees came from a bottomland site covered by a *Populus trichocarpa* T&G—*Juniperus scopulorum* forest. The six remaining trees came from adjacent dry hills covered by a *Juniperus scopulorum-Bouteloua gracilis* (HBK) Lag. ex Steud. woodland.

The dry weight of each tree was determined by the following procedure. The tree was felled and divided into portions with diameters of 0–1, 1–5, 5–10, and greater than 10 cm. These were weighed wet. Samples of material representative of each size were taken, weighed wet, and weighed again after drying to constant weight at 60 C. Dry weight/wet weight ratios for the 0–1, 1–5, 5–10, and 10+ cm size classes were 61, 56, 61, and 61 percent on the dry site and 56, 54, 56, and 53 percent on the wet site. The dry weight of each tree was estimated by multiplying wet weights of each portion by its dry weight/wet weight ratio and summing across portions.

The contribution of photosynthetic organs to the 0–1 cm class was estimated by separating green leaves and twigs from dried samples, weighing, and expressing as a percentage of the 0–1 cm total. The density of dry trunk wood was estimated by dividing sample weights by volumes (about 50 cc) estimated by displacement of water.

The method used to test for the equality of regression lines in both wet and dry sites was to complete three separate regressions using data from, (1) wet sites only, (2) dry sites only, and (3) wet and dry sites combined. Using the symbol SS_i for the residual sum-of-squares in these regressions, the F-statistic for testing equal of regression lines in the two kinds of sites is

---

[1] Department of Botany, Montana State University, Bozeman, Montana 59717.

[2] Department of Statistics, Montana State University, Bozeman, Montana 59717.

$$F = \frac{(SS_3 - SS_1 - SS_2)}{(SS_1 + SS_2)/(N_1 + N_2 - 4)} \quad .$$

This value is compared to entries in an ordinary F table at 2 and $N_1 + N_2 - 4$ degrees of freedom. Although this procedure does not appear in statistical methods texts, it is a simple application of the basic theory for testing linear models (Graybill 1976). The new procedure is a reformulation of the analysis of covariance problem to handle simultaneously a test for both equality of slopes and intercepts (Snedecor 1980).

Results and Conclusions

Although the general climate of our two study sites was nearly identical, their environments were quite different. The climate of the Headwaters of the Missouri areas is dry-continental with an average annual precipitation of 299 mm, average January temperatures of −1 C maximum to −12 C minimum, and average July temperatures of 28 C maximum to 11 C minimum (USDC 1978, Trident). The dry site trees came from a *Bouteloua gracilis* – *Juniperus scopulorum* savannah typical of upland sites of the region. The wet site trees came from a riverside site dominated by old *Populus trichocarpa* trees; they undoubtedly experienced less water stress than the dry site trees due to the site's high water table and shelter from wind and radiation provided by the cottonwoods.

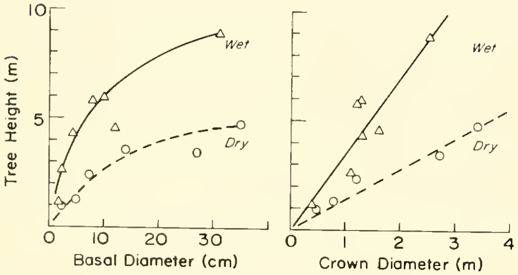


Fig. 1. Wet (△) and dry site (○) tree height-diameter relationships for both basal and canopy diameters differ significantly.

Trees from different environments are expected to have different forms, and indeed they do. (1) Though crown diameter at both sites is linearly related to tree height, at a given crown diameter, dry site trees are only half as tall as wet site trees (Fig. 1). We therefore describe dry site trees as 'broadly conical to hemispheric' and wet site trees as 'spindly.' (2) At both sites supporting structure (basal diameter) increases logarithmically with tree height as is mechanically necessary (Alexander 1971). Still, at a given height, trees of dry sites have bases almost twice as thick as those of wet sites. (3) Because short trees of dry sites and taller trees of wet sites have similar quantities of small leafy twigs per unit of canopy breadth or basal diameter (Table 1), the trees of dry sites have denser foliage (more twigs per vertical meter) than the trees of wet sites. Despite larger reddish heartwood deposits, the density of dry site trunk wood (0.49 ± 0.06 SE g/cc) is not significantly greater than that of wet site wood (0.42 ± 0.05 SE g/cc n = 3, p = 0.05).

Despite the form differences just described, trees of both sites have essentially identical biomasses per unit of basal diameter or canopy diameter. This is demonstrated visually with plots of untransformed total biomass data against tree size (Fig. 2). Regressions of log total aboveground weight (kg) and log

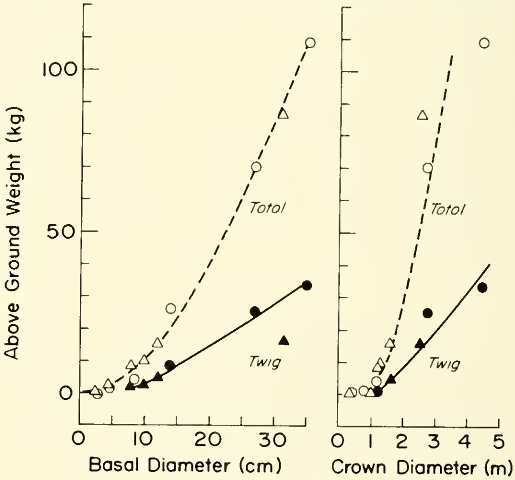


Fig. 2. Aboveground weight-diameter relationships are similar for trees grown on wet (△) and dry (○) sites. Dashed line summarizes total aboveground weight data and the solid line summarizes twig (0–1 cm diameter) weight data.

Table 1. The relationship between tree diameter and aboveground tree weight is shown with regressions of the form log weight (kg or g) = a + b log diameter (cm).

Site	Intercept (a)	Slope (b)	r^2	N	F[1]
		Total weight (kg) basal diameter (cm)			
Wet	1.78	2.21	0.98	7	
Dry	1.55	2.37	0.98	6	
Pooled	1.70	2.26	0.98	13	0.72
		Twig weight (g) basal diameter (cm)			
Wet	1.64	1.78	0.98	7	
Dry	1.60	1.98	0.98	6	
Pooled	1.59	1.91	0.97	13	2.67
		Total weight (kg) canopy diameter (cm)			
Wet	-3.56	3.46	0.80	7	
Dry	-1.94	2.70	0.98	5	
Pooled	-2.55	2.98	0.88	12	0.54
		Twig weight (g) canopy diameter (cm)			
Wet	-2.59	2.75	0.79	7	
Dry	-1.32	2.26	0.97	5	
Pooled	-1.93	2.48	0.85	12	1.19

[1] F testing for difference between wet and dry site regressions. Critical points are 95% = 4.26, 90% = 3.01, 75% = 1.62.

twig biomass (g) against tree size (cm) are summarized in Table 1; in no case did populations differ significantly. Separation of scales from leafy twigs shows that 75 ± 3 and 59 ± 6 SE percent of the leafy twig weight is leaf on dry and wet sites respectively; with six samples from each tree the difference is not statistically significant at P = 0.05. Root-shoot ratios for bottomland trees 5, 12, and 31 cm in diameter were 37, 27, and 26 percent, respectively. Root-shoot ratios appear to generally decline with increasing tree size (Weaver 1974).

Our observation that tall trees and short trees of the same diameter have the same weight is both counter-intuitive and useful. Even if dry site wood is slightly more dense than wet side wood, density differences are insufficient to explain this observation. Instead, the biomass appears to be distributed as if there were a fixed amount of photosynthate per internode which is devoted to diameter growth if it is not expended in height growth. Such allocation on the dry site could be due to adequate light combined with trunk thickening induced by wind stress, while on the wet site it might be due to shade induced etiolation combined with low wind stress (Kramer and Kozlowski 1979, Zimmerman and Brown 1971). Regardless of its cause, the relationship is useful because it suggests that we may apply diameter-biomass relationships developed on one site to other, environmentally dissimilar sites.

Acknowledgments

We gratefully acknowledge the help of K. Boggs, J. Clarke, B. Goulding, S. Gregory, C. Hunt, J. Lichthardt, D. Mullan, J. Newbauer, and K. Striby in harvesting the trees.

Literature Cited

Alexander, R. 1971. Size and shape. Edward Arnold, London. 59 pp.

Brown, J. 1976a. Predicting crown weights for eleven Rocky Mountain conifers. Pages 103–115 *in* Oslo Biomass Studies. International Union of Forest Research Organizations (IUFRO) Congress.

______. 1976b. Estimating shrub biomass from basal stem diameters. Canadian J. Forest Research 6:153–158.

Grayhill, F. 1976. Theory and application of the linear model. Duxbury Press, Belmont, California.

Kira, T., and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jap. J. Ecology 17:70–87.

Kramer, P., and T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York. 811 pp.

Little, E. 1971. Atlas of United States trees, Vol. 1: conifers and important hardwoods. USDA Forest Service Misc. Publ. 1146. U.S. Govt. Printing Off., Washington, D.C. 210 pp.

Snedecor, G., and W. Cochran. 1980. Statistical methods. Iowa State Univ. Press, Ames, Iowa.

Weaver, T. 1974. The growth of two scrub oaks and the cost of their leaves. Montana Acad. Sci. Proc. 34:19-23.

———. 1977. Area-mass relationships for common Montana shrubs. Proc. Mont. Acad. of Sci. 37:54-58.

Weaver, T., and F. Forcella. 1977. Biomass of fifty conifer forests and nutrient exports associated with their harvest. Great Basin Nat. 37:395-401.

U.S. Department of Commerce. 1978. Climatological data. National Oceanographic and Atmospheric Administration (NOAA) Environmental Data Service, National Climatic Center, Asheville, North Carolina.

Zimmerman, M., and C. Brown. 1971. Tree structure and function. Springer Verlag, New York. 336 pp.

A DESCRIPTION OF TIMPIE SPRINGS, UTAH, WITH A PRELIMINARY SURVEY OF THE AQUATIC MACROBIOTA

Thomas M. Baugh[1], Michael A. Nelson[2], and Floyd Simpson[2]

Abstract.— A description of some physical, chemical, and biotic features of Timpie Springs, Utah.

Timpie Springs, Tooele County, Utah, is a spring, pond, marsh complex (Fig. 1) in the southeastern corner of the intersection of Interstate 80 and the Skull Valley Road (Utah Highway 40), Sections 8 and 9, Range 7 W, Township 1S.

This aquatic complex is at an altitude of 1300 m at the northwestern base of the Stansbury Mountains. With the exception of the spring and related mesic habitat, the surrounding area is a typical, xeric, cold-shrub Great Basin sit. Greasewood (*Sarcobatus vermiculatus*), samphire (*Salicornia* sp.), and goat grass (*Aegilops cylindrica*) are the dominant riparian vegetational species.

Present human use of the area includes cattle watering and grazing, fishing, hunting, water withdrawal for road and other construction projects, and water for the impoundments of the adjacent Timpie Wildlife Management Unit.

Human modifications of the area include a galvanized steel flume in the channel connecting the pond with the marsh, a levee separating the marsh from the pond, and a double culvert draining the marsh waters under Interstate 80 into the Timpie Wildlife Management Unit. A well-graded gravel road leads from the Skull Valley Road west to the spring where it joins another well-graded gravel road that follows the foot of the Stansbury Mountain Range in a roughly north-south direction.

Timpie Springs lies at the extreme northwestern tip of the north-south-trending Stansbury Mountain Range, the northern portion of which is characterized as the Garden City

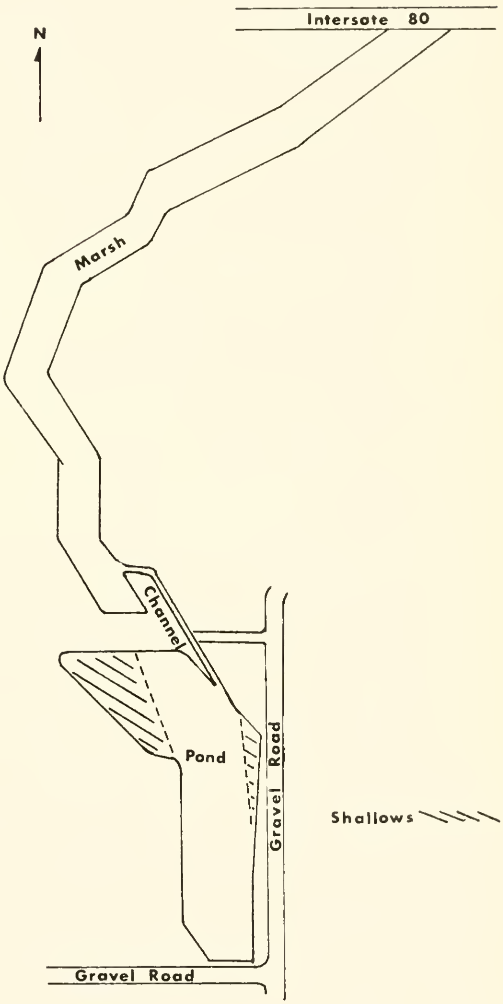


Fig. 1. Schematic of Timpie Springs, Tooele Co., Utah.

---

[1] 1020 Custer Avenue, Ogden, Utah 84404.

[2] 3765 Harrison Boulevard, Ogden, Utah 84403.

Formation (Rigby 1958). The spring issues from the easternmost of a series of faults in the Stansbury Range (Everett 1957). According to Everett (1957) all groundwater in Skull Valley is produced from deposits of lake clays, silts, and gravels intermixed with alluvial deposits. Everett (1957) divides the groundwaters of the valley into a northern saline reservoir and a southern freshwater reservoir. Timpie Springs, originating in the northern reservoir, is estimated to contribute 20,000 tons of salt (total salt in solution) annually to the Great Salt Lake (Eardley 1957).

MATERIALS AND METHODS

Water chemistry values were measured on three occasions at three points in the system: Point A = spring effluent, B = channel, and C = marsh. Chemical constituents were measured by the Hach[3] drop count method and converted to mg/l, where applicable. Temperature was measured with a Weston thermometer (Model 2265).

Fish were captured with long-handled dipnets from within six feet of the banks of the pond and marsh and throughout the length of the channel. The presence or absence and relative abundance of each species was noted.

Aquatic macroinvertebrates were sampled nonquantitatively along the banks of the pond and marsh and throughout the channel. The presence or absence and relative abundance of a species was noted.

Aquatic macroflora was sampled nonquantitatively along the banks of the pond and marsh and throughout the channel. The presence or absence and relative abundance was noted.

RESULTS

POND.— Dabb (1977, 1980) reports the mean depth of the Timpie Springs pond as 5 ft. Our measurements give a surface area of 117,500 ft^2 for the pond. To reach an estimate of total volume, however, it appeared necessary to apply the 5 ft depth only to the main body of the pond. Inclusion of the two main areas of shallows (Fig. 1) gives an inflated figure for volume. The shallow areas account for 34,500 ft^2 of surface area but, at an average depth of one foot, only 34,500 ft^3 of volume. This leaves a surface area of 83,000 ft^2 for the main body of the pond or a volume for the main body of 415,000 ft^3, bringing the total pond volume to 449,500 ft^3. The pond substrate consists mostly of a deep deposit of silt and sand.

CHANNEL.— Discharge from the pond into the channel is 4.6 cfs. Discharge (Q) was calculated by the method described by Reid and Cox (1976):

$$Q(\text{cfs}) = WD_mV_m$$

where Q = discharge (cfs)
D_m = mean channel depth
W = width (ft)
V_m = mean velocity (ft/sec)

---

[3] Hach Chemical Company, Loveland, Colorado.

TABLE 1. Temperature and chemical constituents, Timpie Springs, Tooele Co., Utah.

Site and date in October 1981	Temperature (C)	pH	TH[1]	TA[2]	Ca	Mg	Cl	DO[3]
			mg/l					
A. 3	18.0	7.5	721.5	189.0	395.1	481.0	481.0	5
17	17.8	7.5	652.8	189.0	326.4	326.4	439.5	5
31	17.8	7.5	670.0	189.0	360.7	309.4	451.5	5
B. 3	17.8	8.0	721.5	206.1	377.9	343.6	535.0	8
17	14.4	8.0	670.5	189.0	343.6	326.4	478.8	6
31	14.4	8.0	652.8	189.0	377.9	274.9	—	7
C. 3	16.4	8.0	755.9	171.8	412.3	343.6	530.0	6
17	13.2	8.0	738.7	171.8	395.1	343.6	500.0	7
31	6.1	8.0	687.1	189.0	377.9	309.2	463.6	8

[1] Total hardness
[2] Total alkalinity
[3] Dissolved oxygen

The channel substrate is a loose aggregate of silt and sand above the flume and gravel and rock below the flume to the confluence of the channel with the marsh.

Marsh.— The marsh is a shallow feature with a surface area of 145,945 ft^2, mean depth of about one ft, and a total approximate volume of 145,945 ft^3. It should be noted that marsh depth can vary as much as 50 percent, depending on water use at the Timpie Wildlife Management Unit. The marsh substrate is a deep, loose aggregate of silt, sand, and detritus.

Temperature and chemical constituents.— Temperature and the chemical constituents of Timpie Springs are reported in Table 1. It should be noted that five days of heavy rain preceded the measurements taken on 17 January 1981.

Fish.— Four species of fish *Gila atraria* (Utah chub), *Lucania parva* (rainwater killifish), *Gambusia affinis* (mosquitofish), and *Micropterus salmoides* (largemouth bass), occupy one or more of the components of the Timpie Springs system (Table 2). According to Sigler and Miller (1963), *M. salmoides* and *L. parva* were introduced prior to 1959, *M. salmoides* to develop a sport fishery, and *L. parva* accidentally. It is probable that *G. affinis* was introduced to control mosquitoes. All populations of all species are self-sustaining.

Aquatic macroflora.— The major species of aquatic macroflora are listed in Table 3.

Aquatic macroinvertebrates.— The major aquatic macroinvertebrates of Timpie Springs are listed in Table 4. It should be noted that both the occurrence and numbers of many invertebrates are dependent on seasonal climatic conditions. For example, the week prior to our sampling of 17 October 1981 was cool, with air temperatures ranging from 1.6–4.4 C. Both larval and adult mosquitoes, which had been numerous on 3 October 1981, were conspicuously and pleasantly absent on 17 October 1981.

Table 2. Fishes of Timpie Springs, Tooele Co., Utah.

Species	Location[1]	Frequency[2]
Gila atraria	P	C
	C	C
	M	C
Gambusia affinis	P	VC
	C	C
	M	VC
Lucania parva	P	C
	C	C
	M	VC
Micropterus salmoides	P	C
	C	NP
	M	NP

[1] P = pond, C = channel, M = marsh.

[2] VC = very common, C = common, UC = uncommon, R = rare, NP = not present.

Summary

Timpie Springs is an aquatic system surrounded by typical cold-shrub desert. Major human modification includes the introduction of three species of nonnative fish, the construction of gravel roads, and grazing by cattle. Recreation use includes fishing and some hunting. The spring waters are neces-

Table 3. Major aquatic macroflora of Timpie Springs, Tooele Co., Utah.

Type and genus	Location[1]	Frequency[2]
Pepperwort		
Marsilea sp.	P	C
	C	NP
	M	R
Water nymph		
Najas sp.	P	VC
	C	VC
	M	VC
Blue-green algae		
Enteromorpha sp.	P	VC
	C	C
	M	VC
Oscillatoria sp.	P	C
	C	R
	M	C
Lyngbya sp.	P	VC
	C	R
	M	UC
Green algae		
Chara sp.	P	C
	C	R
	M	VC
Cladophora sp.	P	UC
	C	R
	M	UC
Spriogyra sp.	P	UC
	C	R
	M	UC

[1] P = pond, C = channel, M = marsh.

[2] VC = very common, C = common, UC = uncommon, R = rare, NP = not present.

TABLE 4. Major aquatic macroinvertebrates of Timpie Springs, Tooele Co., Utah.

Type	Order	Location[1]	Frequency[2]
Mosquito	Diptera	P	VC
		C	VC
		M	VC
Dragonfly	Odonata	P	C
Damselfly		C	C
		M	C
Mayfly	Ephemeroptera	P	C
		C	C
		M	C
Backswimmer	Hemiptera	P	VC
		C	C
		M	VC
Crustacean	Amphipoda	P	VC
	(*Hyalella*)	C	VC
		M	VC
Snail (Gastrapoda)		P	VC
		C	VC
		M	VC

[1] P = pond, C = channel, M = marsh.

[2] VC = very common, C = common, UC = uncommon, R = rare.

sary to maintain the aquatic habitats of the closely adjacent Timpie Wildlife Management Unit.

ACKNOWLEDGMENTS

We thank Dr. Earl Smart, Department of Zoology, Weber State College, and Donald Andriano, Jim Johnson, and Glenn Davis, Utah State Division of Wildlife Resources, for their reviews and helpful comments. We thank Dr. Eugene Bosniak, Department of Botany, Weber State College, for his help in identifying the aquatic macroflora.

LITERATURE CITED

DABB, B. 1977. Work study sheets for lakes, reservoirs, and ponds. Report of the Utah State Division of Wildlife Resources, Salt Lake City.

______. 1980. Work study sheets for lakes, reservoirs, and ponds. Report of the Utah State Division of Wildlife Resources, Salt Lake City.

EARDLEY, A. J., V. GVOZDETSKY, AND R. E. MARSELL. 1957. Hydrology of Lake Bonneville and sediments and soils of its basin. Geol. Soc. Amer. 68:1141-1202.

EVERETT, K. R. 1957. Geology and groundwater of Skull Valley, Tooele County, Utah. Unpublished thesis. Univ. of Utah. 92 pp.

REID, G. K., AND R. D. WOOD. 1976. Ecology of inland waters and estuaries. D. Van Nostrand Company, New York. 485 pp.

RIGBY, J. K. 1958. Guidebook to the geology of Utah, No. 13, Geology of the Stansbury Mountains, Tooele County, Utah. Utah Geological Soc. 175 pp.

SIGLER, W. F., AND R. R. MILLER. 1963. Fishes of Utah. Utah State Department of Wildlife Resources, Salt Lake City. 203 pp.

VEGETATION AND SOIL FACTORS IN RELATION TO SLOPE POSITION ON FOOTHILL KNOLLS IN THE UINTA BASIN OF UTAH

Miles O. Moretti[1] and Jack D. Brotherson[2]

Abstract.— Vegetation and soil differences with respect to slope position were studied on foothill knolls in the Uinta Basin of Utah. Plant communities on windswept ridges (top of slope) exhibited several unique characteristics when compared to the other slope communities. These communities at the top and base of slopes were sufficiently different in respect to plant life form composition, plant cover, wind-adapted growth forms, and percent exposed rock that they should be considered separate community types. Mineral concentrations in plant tissue and soil samples declined downslope in some cases and increased in others. Diversity decreased downslope as shrubs became dominant over grasses and forbs. Management of these communities should require special consideration due to the changes in the community structure with slope position.

Vegetation composition, soil factors, and their changes in response to exposure and slope position have received increased attention in recent years (Harner and Harper 1973, Jaynes and Harper 1978, Bloss and Brotherson 1979). The foothill knolls in the Uinta Mountains of Utah are little known ecologically and thus offer opportunities to further our knowledge of such relationships. These foothill knolls, many of which lie adjacent to mountain stream drainages, receive incessant winds, thus creating a unique plant community. Ecological studies of windswept plant communities have generally been restricted to high alpine ridges (Marinos 1978). Little research has been done on such communities at lower elevations (i.e., 2000 and 3000 m).

Anderson et al. (1976) described windswept ridges in south central Wyoming as a vegetative type. The areas so described were ridges that received strong southwesterly winds and had a cover of mat-forming plants. Establishment of the sagebrush-grass community of less windy spots in the area was apparently precluded by the winds. The dominant plant species was Lyal's goldenweed (*Haplopappus lyallii*). Plant cover for the community was estimated to be about 33 percent. Soils in the area were moderately textured (sandy loam to sandy clay loam), with soil depth averaging 17 cm. Exposed rock was twice as great at the top of the slope as at the bottom.

Mineral concentrations in vegetation and soil with respect to slope have not been studied to any extent. Harner and Harper (1973) looked at the increase in mineral concentration in vegetation along a moisture gradient. They concluded that increasing soil moisture permits greater solubility and, therefore, greater absorption of minerals in more productive sites. Fairchild and Brotherson (1980) used topographic position and slope aspect data as independent variables in statistical analyses of shrub habitats in conjunction with mineral concentration in the shrubs and soil.

The objective of this study was to determine the ecological relationships (vegetative and soil) of plant communities, some of which are windswept, with respect to slope position. Knowledge of vegetation and soil differences with respect to slope position should be useful for range managers planning treatment programs (i.e., brush control, range reseeding, etc.). Such would be especially true in areas similar to those described in this study, because much of Utah's big game winter ranges occur in similar topographic locations.

---

[1] Division of Wildlife Resources—State of Utah, 455 West Railroad Avenue, Price, Utah 84501.

[2] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

STUDY AREA

The Uinta Basin is characterized as a broad, elongated, asymmetric basin lying in the northeastern corner of Utah and extending into northwestern Colorado (Brotherson 1979). The central portion of the Uinta Basin is considered a cold desert giving rise to extensive pinyon-juniper forests with a bookcliff type topography (Greenwood and Brotherson 1978). The foothill areas of the Uinta Mountains that lie above the pinyon-juniper forests are dominated by mountain brush. The study area (north and west of Mountain Home, Utah) was located in the mountain brush vegetational zone on three foothill knolls at the foot of the Uinta Mountains. The elevation of the area ranges between 2400 and 2800 m. Climate is highly variable, with cold winters and hot dry summers. Annual precipitation in the area is between 30 and 35 cm, coming mostly in the form of snow during the winter. The area is used as late winter and early spring range for sheep and winter range for elk, deer, and sage grouse.

The communities studied were similar in that all areas display northeast-southwest exposure. Winds generally blow out of the west and are channeled down mountain stream drainages to the west of the study areas.

The windswept side of the communities, especially near the crest of the hill, is dominated by low mat-forming plants, some with the life form of a forb above ground and a shrub below ground. The leeward side is dominated by plants similar to those found on the windward side near the top. The vegetation downslope, where soils are deeper and receive increased moisture from snowdrifts, is dominated by tall shrubs.

METHODS

Three hills were studied within a 26 km^2 area. All had similar exposure, slope, and elevation to insure that meaningful comparisons could be made. Each hill was sampled on both northeast and southwest sides at the top, middle, and bottom slope positions. A total of 90 plots (3 × 3 m) were sampled (30 plots per hill and 15 plots per side). Five plots each were placed along the contour at the top, middle, and bottom of each hill.

Study areas were marked with nylon cord 12 m long with a loop tied every 3 m. The four corners were secured with wooden stakes. Flagging of alternate colors was tied at equal intervals to help insure uniform placement of the 0.25 m^2 quadrats used to subsample each area. Four subsamples were taken within each 3 × 3 m area. Density of shrubs was determined from direct counts of all shrubs within the 0.25 m^2 quadrats. Percent cover was taken in each 0.25 m^2 quadrat for each plant species, rock, bare ground, and litter. Cover values were estimated as suggested by Daubenmire (1959), with some modification. The cover classes: (1)0.01–1.0 percent, (2)1.1–5.0 percent, (3)5.1–25 percent, (4)25.1–50 percent, (5)50.1–75 percent, (6)75.1–95 percent, and (7)95.1–100 percent were weighted to the lower end, in an attempt to make the system more sensitive to large numbers of low-growing species of plants and not to overestimate those plants near the top of the ridges where percentage of exposed rock is greatest. Height of species was also measured. Where a species was represented by less than 5 individuals per plot, all individuals were measured. For species represented by more than 5 individuals per 0.25 m^2 quadrat, 5 individuals were selected at random for measurement.

Soil penetration was measured with a 1-m penetrometer. Depth measures were taken 5 times in each 0.25 m^2 plot. Measurements were taken once at each corner and once in the middle. A total of 20 soil depth measurements was taken within each 3 × 3 m plot.

Soil samples were taken from each corner and middle of each 3 × 3 m plot. These 5 samples were then combined to get a representative sample of the whole plot. Soil samples were analyzed for texture, pH, soluble salts, and mineral ion concentrations (i.e., calcium, magnesium, potassium, sodium, iron, manganese, zinc, copper, nitrogen and phosphorus). Texture was determined as suggested by Bouyoucos (1951). Soil reaction was determined with a glass electrode pH meter. Soluble salts and pH were determined on saturated soil pastes having a 1:1 soil to water ratio (Russell 1948). Organic matter was determined by heating soil samples for 24 hours at 450 C. Differences in weight before and after heating were converted to percent organic matter.

Three soil samples from each slope position were randomly chosen out of the five taken for analysis of mineral concentrations. Individual ion concentration was determined by a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). Potassium, magnesium, calcium, and sodium ions were extracted with a 1 percent neutral normal ammonium acetate solution (Jackson 1958, Hess 1971, Jones 1973). Zinc, manganese, iron, and copper were extracted by using DTPA-diethylenetriaminepenta-acetic-acid extracting agent (Lindsay and Norvell 1969). Soil phosphorus was extracted by sodium bicarbonate (Olsen et al. 1954). Total nitrogen analysis was made using a macro-kjeldahl procedure (Jackson 1958).

Plant samples for chemical analysis were taken randomly at each slope position from within the 3 × 3 m plots. Current year growth for shrubs and all aboveground tissue for forbs and grasses was clipped. The samples were air dried and ashed at 450 C for 24 hours. The ash analysis was made with the atomic absorption spectrophotometer.

Results and Discussion

The environmental factors measured in this study to characterize the communities on foothill knolls near the Uinta Mountains exhibited several general patterns (Table 1). Soil depth was found to be greatest in the midslope position of both the windward and leeward sides (18.5 and 27.7 cm respectively) of the hills. This is possibly the result of sufficient moisture to move the soil from the tops of the ridges but not enough to force the soil outward from the slope base. The leeward position is unique with respect to the other positions as the area receives most of its moisture from the increased accumulation of snow from drifts due to snow accumulation on the leeward side. The areas also have a northeasterly exposure; thus their snow cover remains longer. The result is increased moisture being available to plants for longer periods during critical early growth stages. The leeward position was dominated by Big Sagebrush (*Artemisia tridentata*) and Utah Serviceberry (*Amelanchier utahensis*).

The highest percent exposed rock (61.9 percent) was found on the windward side at the top-slope position; rock then steadily decreased downslope (Table 1). Top positions receive the greatest impact from winds, which sweep away snow and much soil and leave exposed rock. The leeward position shows much less exposed rock (25 percent) but displays a similar trend downslope. Midslope positions probably receive part of the soil blowing in from the windward side. Exposed bare ground and litter cover generally increased downslope. Organic matter and total soluble salts increased slightly downslope (Table 1), and pH showed slight decreases.

Plant life form data (Table 2) give an indication of patterns produced by variation in the relative cover of each life form class. Shrubs increased in relative cover downslope on both sides of the knolls. In contrast, shrub density decreased slightly downslope. This was due to larger plants at the bottom (Table 2) giving a lower density of shrubs but a greater percentage of cover. The midslope position had more species of small shrubs than did the bottom. The shrubs in the top position were small and mat forming, thus giving the lowest cover value for the shrubs (6.0 percent).

Table 1. General environmental factors downslope on windswept communities.

Environmental factor	Slope position windward side			Slope position leeward side		
	Top	Middle	Bottom	Top	Middle	Bottom
Soil penetration	6.7	18.5	16.4	6.7	27.7	21.6
Bare ground (%)	20.1	40.0	41.0	20.8	14.9	21.1
Rock (%)	61.9	38.3	13.2	25.2	4.0	14.7
Litter (%)	27.3	30.5	46.0	41.8	67.7	59.4
Organic matter (%)	6.6	8.1	8.3	7.4	6.6	6.9
pH	7.1	7.0	6.9	6.9	6.9	6.7
Soluble salts (ppm)	181	432	357	207	162	275

Forbs showed their highest cover (13.6 percent) at the top of the windward side of the slope (Table 2) and then decreased downhill. The windward side decrease was much greater than the leeward side. Forbs were poorly represented on the leeward side. The increased density and percent shrub cover on the leeward side probably crowd out forbs.

Grasses showed a relatively constant percent cover on both sides (Table 2). The windward side had a slight decrease in percent cover, but the leeward side had a slight increase. Both had lower percent cover values at the midslope position than at the other two. At the top of the windward side, grasses had a greater percent cover (14.8 percent) than any of the other life form types.

Percent cover for plant species thought to be successful on the windswept ridges (i.e., showed growth forms adapted to windy conditions) were considered together in a group called wind-adapted plants. Plants in this group were mat forming, rhizomatous, or formed rosettes. Cover for species in this group (15.6 percent) was greatest at the top of the windward side (Table 2). The top position of the leeward side had the second largest cover value (8.3 percent). The lowest cover value (1.1 percent) for this group was at the midslope position of the leeward side, which was dominated by tall shrubs. Height of plants was greatest, soil penetration was greatest, and moisture is assumed to be maximal because the largest snowdrifts accumulated there.

The Uinta Basin experienced a drought throughout the first half of 1977, the spring being extremely dry following record low moisture accumulations during the winter. This may explain the low percentage of annuals in the study area. The annuals either did not germinate that year or appeared before the study was initiated.

The average height of all vegetation at each slope position closely paralleled soil depth on the same slope. Vegetation height and soil depth were significantly (positive) correlated ($P < 0.01$), both tending to increase downslope on both windward and leeward sides (Table 2). The leeward side, however, showed an increase in height at the middle position (24.6 cm), then a decrease again at the bottom (19.2 cm). The increase in height can be accounted for by the presence of populations of Utah serviceberry at this midslope position.

A diversity index (Levins 1966, MacArthur 1972) was determined by using percent cover of each plant at each position (Table 2). Diversity decreased on both sides of the knoll downslope. The top position on the leeward side had the highest diversity (9.4). The lowest diversity (3.5) was at the bottom of the leeward side. A Shannon-Weiner (1949) diversity index was also computed and showed similar trends to that of the 1/Sum Pi^2 diversity index.

Cluster analysis (Sneath and Sokol 1973) was used to group slope positions on the basis of vegetative cover (Fig. 1). The bottom-slope positions of both sides of the knolls were the most similar with respect to each other. The top-slope position on the windward side of the knolls was the most different vegetatively of any of the slope positions with respect to all others. This and other evidence indicates that the top of the slope on the windward side is unique with respect to

Table 2. General biotic factors downslope on windswept communities.

Biotic factor	Slope position windward side			Slope position leeward side		
	Top	Middle	Bottom	Top	Middle	Bottom
Life form (% cover)						
Shrub	6.0	21.0	21.4	19.3	26.7	30.0
Forb	13.6	2.0	4.4	4.8	4.4	2.9
Grass	14.8	9.2	12.0	14.6	13.5	15.1
Annual	0.2	0	0.1	0	0.2	0.3
Wind-adapted plants	15.6	3.6	3.7	8.3	1.1	2.6
Shrub density	8.7	7.3	6.0	11.9	12.1	8.9
$\bar{X}$ height (cm)	9.4	16.7	17.1	12.0	24.6	19.2
Diversity (1/Sum P^2)	6.9	4.4	3.9	9.4	6.4	3.5
$\bar{X}$ No. of plant species	14.7	10.3	13.0	17.0	17.7	16.7

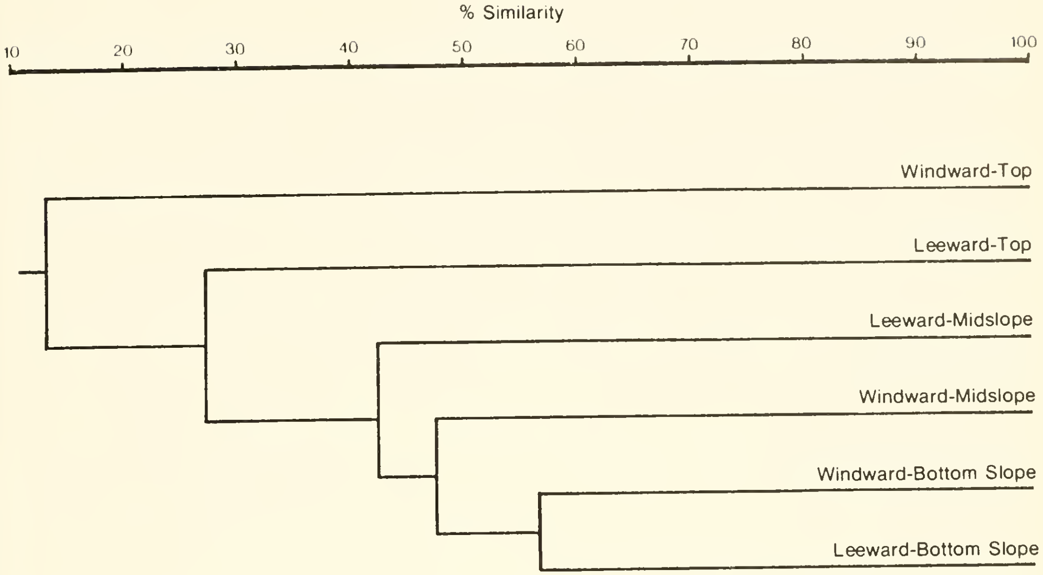


Fig. 1. Phenogram of the relationships between the slope position communities. Cluster is based on species cover values.

the remainder of the hill. There exists an area that could well be classified as a separate vegetation type with regard to the surrounding plant community. Anderson et al. (1976) stated that windswept communities are restricted to the ridges where the more competitive sagebrush can't tolerate the desiccating winds and rockier soil. The areas provided habitat for low, mat-forming plants. The area had an average plant cover of 33 percent and compares closely to this study, which has an average plant cover in the same position of 34.6 percent.

The average number of plants per slope position used to develop a prevalent species list is shown in Table 3. The windward side

Table 3. Prevalent species (% cover) for foothill knolls in the Uinta Basin, Utah.

	Slope position windward side			Slope position leeward side		
Species	Top	Middle	Bottom	Top	Middle	Bottom
Artemisia tridentata	0.0	13.6	18.3	11.5	11.8	23.8
Xanthocephalum sarothrae	0.4	0.4	0.0	2.2	0.0	0.9
Amelanchier utahensis	0.0	0.4	0.4	2.1	5.9	0.0
Phlox bryoides	10.3	1.7	3.4	0.4	0.6	1.1
Koeleria cristata	1.4	0.4	2.2	0.1	1.6	1.1
Stipa comata	4.6	0.0	1.0	2.6	0.8	0.6
Antennaria parvifolia	0.0	0.0	0.2	0.3	0.0	0.4
Bouteloua gracilis	1.6	1.1	0.0	4.1	0.0	0.0
Poa fendleriana	0.0	1.0	1.1	4.0	0.0	0.8
Artemisia cana	0.8	0.2	0.1	0.8	0.0	0.0
Artemisia frigida	4.6	1.1	0.0	0.6	0.0	0.0
Agropyron spicatum	4.4	4.8	6.1	1.7	8.1	8.8
Eriogonum heracleoides	0.0	0.0	0.1	1.0	1.1	0.0
Berberis repens	0.0	0.0	0.0	0.9	0.4	0.0
Penstemon sp.	0.0	0.0	0.0	0.6	1.6	0.2
Symphoricarpos oreophilus	0.0	0.0	1.7	0.6	8.0	2.6
Elymus ambiguus	1.8	1.8	1.5	0.0	0.0	4.2
Purshia tridentata	0.0	0.0	0.0	0.0	0.0	2.3
Cercocarpus montanus	0.0	4.9	0.0	0.0	0.0	0.0
Chrysothamnus greenei	0.0	0.0	0.4	0.0	0.0	0.0

had an average of 12.7, but the leeward side was much higher with 17.1 species.

A prevalent species list was developed for each slope position based on the average number of species per position and percentage cover (Table 3). Plant cover was generally low at most positions. Forbs and grasses exhibited reduced growth due to soil droughtiness, thus contributing less to the overall percent cover. Total percent cover increased downslope. The lowest percent plant cover (37.0 percent) on the leeward side was higher than the highest percent cover value (36.7 percent) on the windward side. The largest percent plant cover (46.4 percent) was at the bottom position of the leeward side of the knoll but had the highest concentration of a single species to the total. Big sagebrush (*Artemisia tridentata*) provided 23.8 percent cover (51 percent of the total plant cover for the bottom position). The highest percent cover on the windward side was again at the bottom position (36.7 percent), where big sagebrush (18.3 percent absolute cover) contributed 50 percent of the total cover (Table 3).

Two species were found in study plots at all slope positions: Moss phlox (*Phlox bryoides*) and Bluebunch wheatgrass (*Agropyron spicatum*). Big sagebrush exhibited the highest percent cover of any species at all except on the top slope position on the windward side, where it did not occur. The sites on the windward side were dominated by Moss phlox (10.3 percent); Needle and Thread (*Stipa comata*), (4.6 percent cover); Fringed sagebrush (*Artemisia frigida*), (4.6 percent); and Bluebunch wheatgrass (4.4 percent).

Soil ion concentrations ranged from a low of 0.6 ppm for copper at the midslope position on the leeward side to a high of 5947 ppm for calcium at the midslope position on the windward side (Table 4). Concentrations of minerals between windward and leeward sides generally followed similar patterns. Zinc is the only ion to decrease downslope on one side and increase downslope on the other. Calcium and iron generally decreased downslope, but phosphorus, manganese, nitrogen, magnesium, and potassium showed increases (Table 4). Nitrogen, calcium, magnesium, and potassium occurred in high concentration on both exposures. Epstein (1972) suggested that for soils to maintain healthy plant tissue, a soil concentration of 200 ppm of phosphorus is required. Both exposures had 10 percent or less of this concentration of phosphorus in the soil.

Mineral concentrations in plant tissue remained level or generally increased downslope on the windward and leeward exposures. Ion concentration in the plants ranged from 8 ppm for copper on the top position of the leeward side to 23,000 ppm for nitrogen at the midslope position of the leeward side (Table 5). The high concentration of nitrogen in the midslope position on the leeward side corresponds with the highest percent litter (67.7 percent). This can be attributed to an increase in nitrogen fixation by free-living microorganisms in and under litter mats (Charley 1977).

The mean ion concentration for copper in plant tissue was considerably lower (10 ppm) than the mean of 28.9 ppm found by Brothersen and Osayande (1980) in True Mountain Mahogany (*Cercocarpus montanus*) 30 km to

TABLE 4. Soil mineral concentration downslope on windswept communities.

Minerals (ppm)	Slope position windward side			Slope position leeward side		
	Top	Middle	Bottom	Top	Middle	Bottom
Zinc	1.3	1.4	1.5	2.1	1.6	1.2
Iron	16.4	10.9	14.5	21.2	21.1	17.0
Phosphorus	11.9	10.8	15.8	13.9	13.8	20.1
Manganese	12.0	11.3	18.0	12.7	15.0	18.7
Copper	0.8	0.9	1.2	0.7	0.6	0.9
Sodium	42.0	42.3	41.0	40.3	35.7	41.0
Nitrogen	2000.	1400.	1800.	2100.	2000.	1900.
Calcium	3971.	5947.	3790.	3378.	2853.	2558.
Magnesium	168.	606.	491.	223.	230.	338.
Potassium	169.	232.	300.	208.	200.	288.

the southeast in the pinyon-juniper woodland. The concentration is well below the 20 ppm suggested by Baker (1974) as being toxic to some ruminant animals. The highest concentrations of copper (11 ppm) were found at the bottom positions of both exposures.

Concentrations of the macronutrients (iron, phosphorus, nitrogen, calcium, magnesium, and potassium) in the plants were high and the concentrations of micronutrients were low. Ion concentrations in the plants were found to be adequate for higher plants to maintain a healthy condition (Epstein 1972). Minerals concentrated in plant tissue varies in meeting the nutritional requirements of sheep and cattle that graze the area. Most minerals met or exceeded the mineral requirements of sheep and cattle (NRC 1976). Copper (8–11 ppm) and iron (308–706 ppm) were the only two elements present in quantities considered to be toxic. Copper within the 8–25 ppm range is considered to be toxic to sheep. Iron exceeded the toxic level for cattle (400 ppm) in three of the six slope positions. Because the mineral concentration in plant tissue was determined from a combination of all the plants within each area, some plant species high in these minerals may be unpalatable to animals and not part of their diet.

The ratio of mineral concentration in the plant versus the soil shows to what extent the plants take up and concentrate the minerals (Table 6). The highest ratio was found for phosphorus, which was 108 to 176 times more concentrated in plant tissue than in the soil. The lowest ratio for mineral concentration was for manganese (2.1) at the bottom-slope position of the leeward side. Manganese had the lowest concentration ratio for all the minerals at all of the positions (Table 6).

Potassium had the second highest ratio, ranging from a low of 48.3 at the bottom-slope position to a high of 81.0 at the top, both on the windward side. Potassium, the only monovalent cation essential for all higher plants, is inefficient as a cofactor in enzyme systems and plants have evolved the ability to take up large concentrations from the soil (Epstein 1972).

The mineral concentrations in the soil and plants, plant life form, and other environmental factors were subjected to correlation analysis (Table 7). Several significant correlations developed within and among the groups in relation to changes downslope. Soil depth was positively correlated with plant height; thus, as soil became deeper downslope, plant height increased. Soil depth was negatively correlated with plant density; thus, as shown earlier, shrub density was highest at the top of the hills where soil was shallowest (Table 7A).

Shrubs as a life form were negatively correlated with forbs. Consequently, as shrubs increased downslope forbs decreased (Table 7A). Cover for forbs (13.6 percent) was highest at the top position on the windward side, where shrub cover (6.0 percent) was lowest. Shrubs were also highly correlated with plant height. Forbs were negatively correlated with height downslope. Percent cover by forbs (13.6 percent) was highest at the top position on the windward side, where plant height was lowest (9.4 cm). Grasses were not correlated either positively or negatively with either shrubs or forbs. Percent cover by grasses was not associated with plant height

Table 5. Plant mineral concentrations downslope on windswept communities.

Minerals (ppm)	Slope position windward side			Slope position leeward side		
	Top	Middle	Bottom	Top	Middle	Bottom
Zinc	14.0	23.7	25.0	15.7	20.7	23.7
Iron	308.	491.	627.	379.	366.	706.
Phosphorus	1,400.	1,900.	2,200.	1,500.	1,900.	2,400.
Manganese	35.	38.	70.	45.	67.	40.
Copper	10.	9.	11.	8.	9.	11.
Sodium	226.	250.	287.	237.	249.	287.
Nitrogen	20,000.	21,000.	21,000.	20,000.	23,000.	21,000.
Calcium	7,800.	9,400.	15,400.	9,300.	10,000.	8,700.
Magnesium	1,800.	2,400.	2,800.	2,100.	2,300.	2,000.
Potassium	13,700.	13,600.	14,500.	13,300.	13,400.	14,200.

as were shrubs and forbs. Forbs as a life form were not positively correlated with any factor and grasses were not negatively correlated with any factor. Plant height was negatively correlated with density because the highest density was at the top of the ridges where height was lowest.

Soil minerals tended to be more positively than negatively associated with the other factors (Table 7B). Grasses were positively correlated with phosphorus and nitrogen downslope. Two studies have shown that an increase in phosphorus and nitrogen increases the amount of biomass produced on rangelands (Barrett 1979, Wight 1976). Magnesium was the only soil mineral positively correlated with shrubs. Copper was highly correlated with several factors in the soil and plants (Table 7B). It was the only mineral to be correlated either positively or negatively between the plant and soil.

As above, mineral concentrations in plants were also more positively than negatively correlated with the other factors. Zinc, iron, and phosphorus were positively associated with shrub cover. These minerals increased downslope as did percent cover by shrubs. Forbs showed the reverse trend, with percent cover by forbs decreasing downslope as zinc, iron, and phosphorus increased. Nitrogen in plants was positively correlated with plant height.

Vegetative and soil differences in areas subjected to high winds develop characteristics that distinguish them from the surrounding plant community. The tops of the windswept ridges have several unique features (i.e., percent exposed rock, soil depth, plant height, plant cover, and composition of life form). Management of these areas for livestock or wildlife should include special considerations. The windswept ridges during winter are often snow-free while the surrounding areas are covered. This would tend to concentrate animals in these areas and cause overgrazing. Also, these areas are the first to green up in the spring due to the exposure, which may be why animals graze these areas while plant carbohydrates are low.

Improvements or rehabilitation of these areas (i.e., brush control, range reseeding, etc.) by range managers must be looked at closely. Anderson et al. (1976) showed in Wyoming that windswept areas had a different relative cover by palatability class than the surrounding vegetation type, even though both areas rated fair for range condition. Plant types and species used to improve these areas must be able to withstand the harsh environment of the windswept ridges. Life forms of the plants should show adaptation (i.e., low, mat forming, rhizomatous, drought- and cold-hardy grasses or forbs) able to withstand the unique environments of the sites.

Revegetation attempts in these areas would best be achieved by planting mixtures of seeds rather than using single seed species in reseeding projects. Mixtures would allow greater variability in the plant resource in meeting the needs of an ever-changing and varied habitat. Jaynes and Harper (1978) stated that species of undesirable forage value may be the only plant species available to meet the criteria of areas with harsh environments (such as windswept ridges). Vegetative cover to prevent erosion may have priority over palatable forage in certain areas.

Table 6. Plant and soil ratios of mineral concentrations with regard to slope position.

Minerals	Slope position windward side			Slope position leeward side		
	Top	Middle	Bottom	Top	Middle	Bottom
Zinc	10.8	16.9	17.9	7.5	12.9	19.8
Iron	18.8	45.1	43.2	17.9	17.3	41.5
Phosphorus	117.6	175.9	139.2	107.9	137.7	119.4
Manganese	2.9	3.4	3.9	3.5	4.5	2.1
Copper	12.5	10.0	9.2	11.4	15.0	12.2
Sodium	5.4	5.9	7.0	5.9	7.0	7.0
Nitrogen	10.0	15.0	11.7	9.5	11.5	11.1
Copper	2.0	1.6	4.1	2.8	3.5	3.4
Magnesium	10.7	4.0	5.7	9.4	10.0	5.9
Potassium	81.0	58.6	48.3	63.9	67.0	49.3

Management of windswept communities and ranges with rolling hill country, as discussed in this paper, should be preceded by a careful study of the vegetative and soil differences to insure successful management programs.

Literature Cited

Anderson, D. L., W. K. Ostler, C. Freeman, and K. T. Harper. 1976. Vegetation of the proposed China Butte coal strip mine. Rocky Mountain Energy Co. Report 1976: 4–23.

Baker, D. E. 1974. Copper: soil, water, plant relationships. Federation Proc. 33:118–1193.

Barrett, M. W. 1979. Evaluation of fertilizer on pronghorn winter range in Alberta. J. Range Manage. 32(1):55–59.

Bloss, D., and J. Brotherson. 1979. Vegetation response to a moisture gradient on an ephemeral stream in central Arizona. Great Basin Nat. 39:161–176.

Boyuoucos, G. J. 1951. A recalibration of the hydrometer method for making mechanical analysis of soils. J. Agron. 43:434–438.

Brotherson, J. D. 1979. Ecological and community relationships of *Eriogonum corymbosum* (Polygonaceae) in the Uinta Basin, Utah. Great Basin Nat. 39:177–191.

Brotherson, J. D., and S. T. Osayande. 1980. Mineral concentrations in true mountain mahogany and

Table 7. Correlation coefficients of environmental and biotic factors with respect to each other: Section A, life form, general vegetative and site factors; Section B, mineral concentration in the soil; Section C, mineral concentration in the plants; subscript "p," mineral concentrations in plant; subscript "s," mineral concentrations in soil; superscripts "2,3,4," significant levels as follows: 2 = 0.05, 3 = 0.02, 4 = 0.01.

Factor	Positive correlations	Negative correlations
A		
Shrub	Soil depth^2, height^4	Forb^4
Forb		Zn^2_p, shrub^4
Grass	Fe^4_s	
Annual		
Plant height	Soil depth^4, Zn^2_p, shrub^4	Plant density^3
Plant density	Fe^3_s,	Soil depth^4, height^3
Organic matter	Cu^2_s, Mg^4_s, Mg^4 soluble salts^4, Zn^4_p	
pH	Ca^4_s, Ca^2_p, Mg^2_p	Fe^4_s, P^2_s, Cu^3_s, Na^3_s, K^2_s, Fe^4_p, P^3_p, plant
Soluble salts	Cu^4_s, Ca^2_s, Mg^4_s organic matter^4, Zn^4_p,	
Soil depth	shrub^2, height^4	Plant density^4
B		
Zinc		
Iron	N^3_s	Ca^2_s, pH^4, Mg^2_p, Plant density^3
Phosphorus	Fe^2_s, Mn^4_s, Na^2_p,	Ca^2_s, K^3_s, pH^2
Manganese	P^4_s, K^4_s, Na^2_p	
Copper	Na^4_s, Mg^4_s, K^4_s, organic matter^2, soluble salts^3, Zn^4_p, Fe^4_p, Cu^2_p, p^3_p	pH^3
Sodium	Cu^4_s, Fe^3_p, P^2_p, Cu^2_p	pH^3
Nitrogen	Fe^3_s	
Calcium	pH^4, soluble salts^2, Mg^3_p	Fe^2_s, P^2_s
Magnesium	Cu^4_s, organic matter^4, soluble salts^4, Zn^4_p, Fe^2_p	
Potassium	P^3_s, Cu^4_s, Fe^4_p, Na^2_p	pH^2
C		
Zinc	Cu^4_s, Mg^4_s, organic matter^4, soluble salts^4, P^4_p, Cu^4_p, Height^2	Forb^2
Iron	Cu^4_s, Na^3_s, Mg^2_s, K^4_s, P^4_p, Cu^2_p	pH^4
Phosphorus	Cu^4_s, Na^2_s, Mg^2_s, Zn^4_p, Fe^4_p, Cu^4_p, K^2_p	pH^3
Copper	Cu^2_s, Na^2_s, Zn^4_p, Fe^2_p, P^4_p	pH^4
Sodium	P^2_s, Mn^2_s, K^2_s	
Calcium	Mn^4_s, Mg^4_s	Plant density^2
Magnesium	Ca^3_s, pH^3, Mn^3_p, Ca^4_p	Fe^2_s
Potassium	P^2_p	

Utah juniper and in associated soils. J. Range Manage. 33:182–185.

CHARLEY, J. L. 1977. Mineral cycling in rangeland ecosystems. *In* R. E. Sosebee, ed., Range plant physiology. Society for Range Management, Range Science Series No. 4.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational and analysis. Northwest Sci. 33:43–46.

EPSTEIN, E. 1972. Mineral nutrition of plants: principles and perspectives. John Wiley and Sons, New York. 412 pp.

FAIRCHILD, J. AND J. D. BROTHERSON. 1980. Microhabitat relationships of six major shrubs in Navajo National Monument, Arizona. J. Range Manage. 33:150–156.

GREENWOOD, L. C., AND J. D. BROTHERSON. 1978. Some ecological relationships between pinyon-juniper and birchleaf mountain mahogany stands. J. Range Manage. 31(3):164–168.

HARNER, R. F., AND K. T. HARPER. 1973. Mineral composition of grassland species of the eastern Great Basin in relation to stand productivity. Can. J. Bot. 51:2037–2046.

HESS, P. R. 1971. Textbook of soil chemical analysis. Chem. Publishing Co., ew York.

ISAAC, R. A., AND J. D. KERBER. 1971. Atomic absorption and flame photometry: techniques and uses in soil, plant, and water analysis. Pages 17–38 *in* L. M. Walsh, ed., Instrumental methods for analysis of soils and plant tissue. Soil Sci. Soc. Amer. Wis.

JACKSON, M. L. 1958. Soil chemical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

JAYNES, R. A., AND K. T. HARPER. 1978. Patterns of natural revegetation in arid southeastern Utah. J. Range Manage. 31:407–411.

JONES, J. B. 1973. Soil testing in the United States. Comm. Soil Sci. Plant Anal. 4:307–322.

LEVINS, R. 1966. The strategy of model building in ecology. Am. Sci. 54:412–431.

LINDSAY, W. L., AND W. A. NORVALL. 1969. Development of a DTPA micronutrient soil test, Agron. Abstracts. Equilibrium relationships of Zn++, Fe++, Cu++, and H+ with EDTA and DTPA in soil. Soil Sci. Soc., Amer. Proc. 33:62–68.

MACARTHUR, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York. 251 pp.

MARINOS, N. G. 1978. Fellfields and cushion plants of the Rockies. Utah Sci. 6:68–72.

NATIONAL RANGE COUNCIL. 1976. Nutrient requirements of beef cattle. 5th ed. National Academy of Sci., Washington, D.C. 56 pp.

———. 1976. Nutrient requirements of sheep. 5th ed. National Academy of Sci., Washington, D.C. 72 pp.

RUSSELL, D. A. 1948. A laboratory manual for fertility students, 3d ed. Wm Brown Co., Dubuque, Iowa. 56 pp.

SHANNON, C. E., AND W. WEINER. 1949. The mathematical theory of communication. University of Illinois Press, Urbana. 65 pp.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy, the principles and practices of numerical classification. W. H. Freeman and Co., San Francisco, California. 547 pp.

WIGHT, J. R. 1976. Range fertilization in the northern Great Plains. J. Range Manage. 29:108–185.

WEATHER CONDITIONS IN EARLY SUMMER AND THEIR EFFECTS ON SEPTEMBER BLUE GROUSE (*DENDRAGAPUS OBSCURUS*) HARVEST

Joy D. Cedarleaf[1], S. Dick Worthen[2], and Jack D. Brotherson[1]

Abstract.— Relationships of temperature and precipitation to the reproductive success of blue grouse (*Dendragapus obscurus*) were investigated. Maximum and minimum temperatures followed similar patterns during the years 1976–1981 and showed no patterns relative to hatching success. Precipitation data, however, was variable. When significant amounts of precipitation fell during the last three weeks of the hatching period, chick survival and, therefore, recruitment were adversely affected. We suggest that precipitation occurring at the end of the hatch period reduces the September harvest of birds.

Blue grouse (*Dendragapus obscurus*) inhabit fir forests in many western states (Beer 1943). The range of this species is closely associated with the distribution of true fir (*Abies*) and Douglas fir (*Pseudotsuga*) in western North America (Beer 1943). Blue grouse depend on conifer cover in winter and on shrubs, forbs, and grasses during the spring and summer (Rogers 1968). Most blue grouse are migratory, moving from spring and summer ranges in open meadows to timbered wintering areas at higher elevations in winter (Johnsgard 1973).

The quality of breeding habitat seems to affect the number of breeding birds (Zwickel et al. 1968). In the latter study, grazed and ungrazed habitats and their effects on blue grouse breeding success were compared. There was greater breeding success on ungrazed areas (Zwickel et al. 1968). Herbaceous vegetation that suffers under heavy grazing is used by the birds for food and cover. Good grazing practices are important for the maintenance of blue grouse populations (Mussehl 1963).

Zwickel and Bendell (1967) suggest that another important factor in regulating the population densities of blue grouse is the dispersal of the juvenile birds to winter ranges. They also noted that temperature and moisture did not seem to affect the two broods they observed.

As a species, blue grouse have become important upland game birds in the state of Utah in recent years (Bunnell et al. 1977). After reestablishing and lengthening the hunting season, efforts are presently being made to determine the general status of populations as well as population trends (Rogers 1963). Because of their solitary nature and the dense cover they inhabit, their population densities are difficult to estimate (Johnsgard 1973). Fluctuating population densities and inconsistencies of hatch makes management and utilization of the blue grouse resource difficult. In this study, temperature and precipitation were compared to the hatching success of blue grouse to see if either of these factors affected the age and number of birds harvested.

Study Site

The study area lies along the west slopes of the Wasatch Mountains of central Utah (the Wasatch Front), extending from American Fork Canyon on the north to Hobble Creek Canyon on the south. This represents a distance of some 50 km (30 m). Here several major canyons and their drainage basins extend eastward into the mountains away from the Wasatch Front. Coniferous forests (subalpine fir zone), in which Douglas fir and species of true fir are prominent, occur in the drainage basins and along the canyon slopes. The meadow and open areas associated with this zone contain shrubs such as chokecherry (*Prunus* spp.), serviceberry (*Amelanchier* spp.), snowberry (*Symphoricarpos* spp.) and elderberry (*Sambucus* spp.), as well as various forbs and grasses.

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

[2] Division of Wildlife Resources—State of Utah, 1115 North Main, Springville, Utah 84663.

Materials and Methods

Ten weather stations were chosen to represent the study area. These stations were all located in Utah County, Utah, and varied in elevation from 1370 m (4497 ft) to 1720 m (5640 ft). The data collected at these stations were obtained from the National Climatic Center in Asheville, North Carolina. The maximum and minimum temperatures of each week for the months of May, June, and July were summed and averaged for each of the ten weather stations. The precipitation data for this time period were also summed and averaged. The weekly precipitation and temperature averages were then plotted against the weekly hatching curve for the same year. This was done for the years 1976–1981. The weather stations located in the same general vicinity were grouped together and those figures were then averaged and plotted against the hatch data. The precipitation received at each station was tallied separately, averaged, and plotted on the graph against the hatch curve (Figs. 1–2).

Checking stations were set up to gather harvest information. Wings were used to determine the sex and age of each bird. Three stations were located in canyons (American Fork, Provo, and Hobble Creek) that contained populations of blue grouse. Each station was operated from 9:00 a.m. until 7:00 p.m. on each of the two days of the opening weekend of the grouse season. One wing was

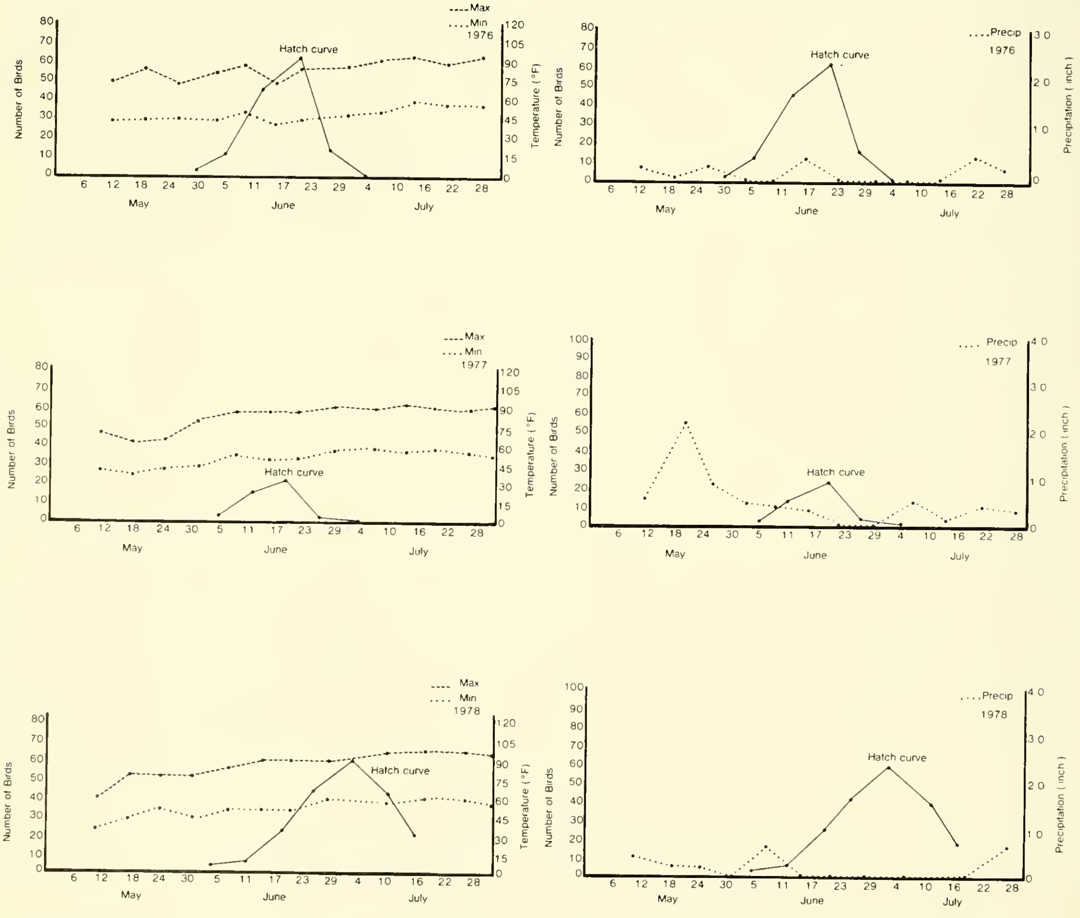


Fig. 1. Temperature and precipitation plotted against the number of birds in the hatch curve for the years 1976–1978.

collected from each blue grouse brought to the station, as well as hunter success information. In addition to the check stations, wing barrels were set up to gather wings during the first two weeks of the hunt.

Wings collected at the stations and the wing barrels were analyzed by Division of Wildlife Resources biologists to determine sex and age of the birds (Bunnell et al. 1977). Additional data were gained from the juvenile wings by back dating to the time of the hatch (Schladweiler 1970).

Results and Discussion

The maximum and minimum temperatures generally followed the same pattern each year (Figs. 1–2). None of the years or stations contained extreme maximum or minimum temperatures. The years 1976 to 1979 had little or no precipitation during the latter part of the hatch period, but the years 1980 and 1981 had precipitation during the last two weeks of the hatch period (Figs. 1–2).

The hatch curve as well as the percentage of juveniles contained in the harvest were determined from the wings collected (Schladweiler 1970). A high number of juveniles (75 percent) in the harvest indicates good or high production and recruitment into the population. In the years 1980 and 1981, 48 percent of the birds harvested were juveniles. In the years 1976, 1977, 1978, and 1979 the harvest included 78 percent, 63 percent, 66 percent, and 73 percent juveniles, respectively. These values are believed to give good indication as to population composition during these years. If the percentage of the

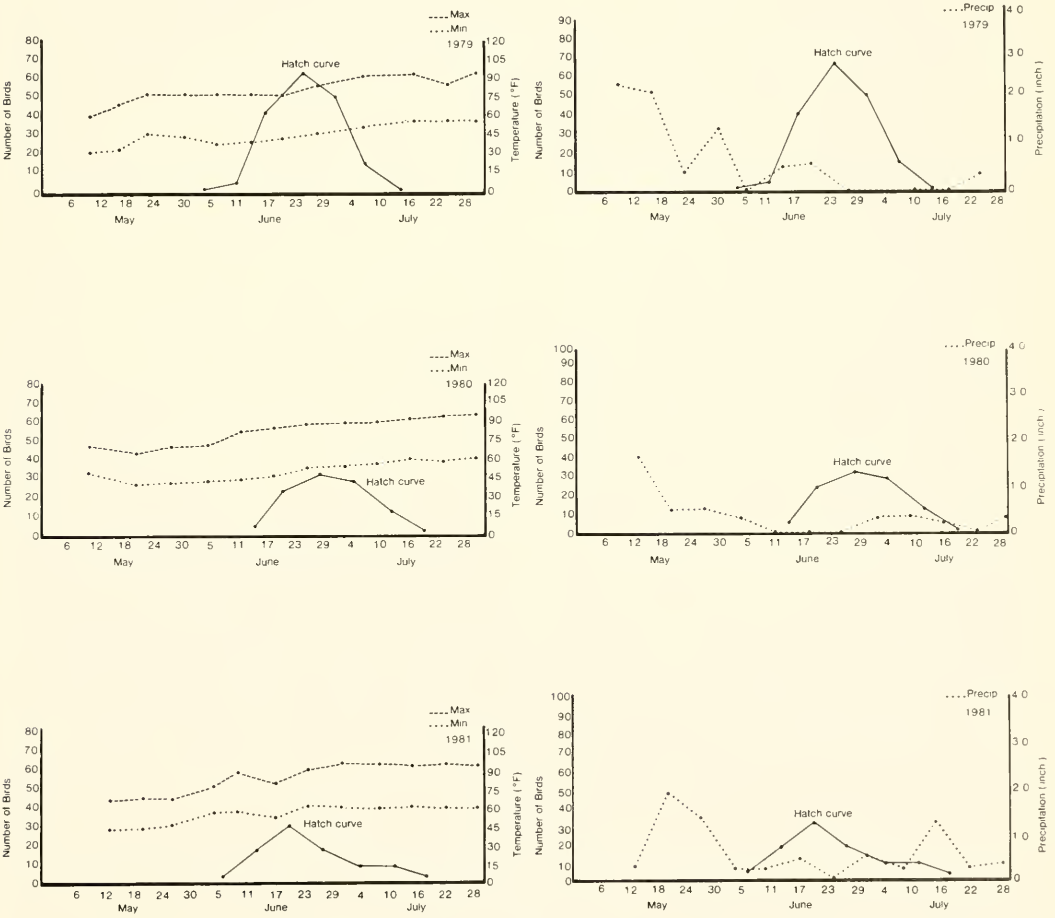


Fig. 2. Temperature and precipitation plotted against the number of birds in the hatch curve for the years 1979–1981.

harvested juvenile birds is low, then the population is considered down. The years 1980 and 1981 had a low percentage of juvenile birds when compared to the years 1976 to 1979. If we graph the precipitation during the last three weeks of the hatch period, and the percentage of juveniles in the harvest against time in years, an interesting relationship appears (Fig. 3). The two lines become mirror images of one another. Further, if percentage of juveniles in the harvest and total precipitation during the last three weeks of the hatch period are graphed against each other (Fig. 4), the relationship shown is statistically significant ($P < 0.05$). As the precipitation during this period increases, the percent of juveniles in the harvest decreases. This suggests that precipitation late in the hatch period affects chick survival and recruitment.

Zwickel (1967) suggests that moisture and cold weather do not affect the chicks. He also suggests that the dispersal of the juveniles to their winter ranges is the major population regulating factor. The dispersal of the juveniles would seem to affect each brood separately and therefore should not have an overall effect on population.

Factors which could reduce the proportion of juvenile birds in the harvest could be precipitation, temperature, or a combination of both. Our study suggests that precipitation during the hatching season may be responsible for few juveniles in the harvest. Extreme amounts of precipitation or extremely low temperatures during a couple of days late in the hatching period could affect the population drastically. This affect on the population may not be shown in our data because it would be masked by the averages of temperature and precipitation.

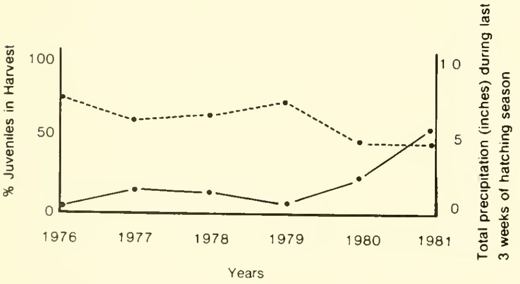


Fig. 3. Percent juveniles in the harvest plotted against the total precipitation (inches) during the last three weeks of the hatching season for the years 1976–1981.

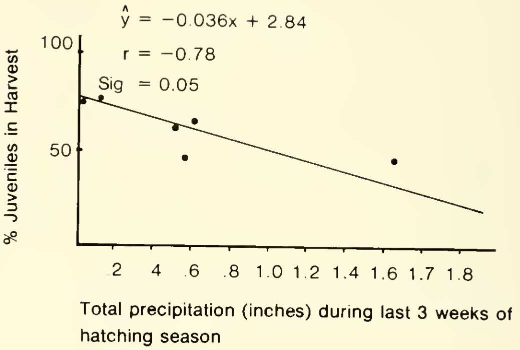


Fig. 4. Percent juveniles in the harvest plotted against the total precipitation (inches) during the last three weeks of the hatching season.

Additional studies are needed to determine the specific regulating factors of blue grouse populations. This study seems to indicate that the amount of moisture received during the last part of the hatching period can affect the number of juveniles entering the population.

Literature Cited

Beer, J. 1943. Food habits of the blue grouse. J. Wildlife Manage. 7:32–44.

Boag, D. A. 1963. Significance of location, year, sex, and age to the autumn diet of blue grouse. J. Wildlife Manage. 27:555–562.

Bunnell, D. S., J. S. Rensel, J. F. Kimball, and M. L. Wolfe. 1977. Determination of age and sex of dusky blue grouse. J. Wildlife Manage. 41:662–666.

Fowle, C. D. 1960. A study of the blue grouse on Vancouver Island, B.C. Canadian J. Zool. 38:701–713.

Johnsgard, P. A. 1973. Dusky blue grouse. Pages 175–192 *in* Grouse and quail of North America. Univ. of Nebraska Press.

Mussehl, T. W. 1963. Blue grouse brood cover selection and land use implications. J. Wildlife Manage. 27:579–554.

Rogers, G. B. 1963. Blue grouse census and harvest in the United States and Canada. J. Wildlife Manage. 27:579–585.

———. 1968. The blue grouse in Colorado. Colorado Game, Fish, and Parks Dept., Game Research Division Technical Publication No. 21.

Schladweiler, P., T. W. Mussehl, and R. J. Greene. 1970. Age determination of juvenile blue grouse by primary development. J. Wildlife Manage. 34:649–652.

Smith, N. D., and I. O. Buss. 1963. Age determination and plumage observations of blue grouse. J. Wildlife Manage. 27:566–578.

TERVORT, P. 1976–1979. Upland game inventory report. Utah Division of Wildlife Resources. P.R. Project W-65-R.

WORTHEN, S. D. 1980 and 1981. Upland game inventory report. Utah Division of Wildlife Resources. P.R. Project W-65-R.

ZWICKEL, F. 1972. Some effects of grazing on blue grouse during summer. J. Wildlife Manage. 36:631–634.

———. 1967. Some observations of weather and brood behavior in blue grouse. J. Wildlife Manage. 31:563–567.

ZWICKEL, F., AND J. F. BENDELL. 1967. Early mortality and the regulation of numbers in blue grouse. Canadian J. Zool. 45:817–851.

ZWICKEL, F., I. O. BUSS, AND J. H. BRIGHAM. 1968. Autumn movements of blue grouse and their relevance to populations and management. J. Wildlife Manage. 32:456–467.

DESCRIPTION OF THE FEMALE OF *PHALACROPSYLLA HAMATA* (SIPHONAPTERA: HYSTRICHOPSYLLIDAE)

R. B. Eads[1] and G. O. Maupin[1]

Abstract.— The previously unknown female of *Phalacropsylla hamata* Tipton & Mendez is described and an allotype is designated. A key is provided to aid in distinguishing females of this genus.

The genus *Phalacropsylla* includes an interesting assemblage of species adapted to high altitudes. Described species include *P. paradisea* Rothschild 1915, *P. allos* Wagner 1936, *P. nivalis* Barrera & Traub 1967, *P. hamata* Tipton & Mendez 1968, and *P. oregonensis* Lewis & Maser 1978. With the exception of *allos,* these nest fleas have not been commonly collected, even during extensive ectoparasite studies (including nest examinations) within the known range of the genus in the western United States and Mexico. Host records suggest that wood rats, *Neotoma* spp., and closely associated rodents and lagomorphs are normal hosts of the *Phalacropsylla.*

Phalacropsylla hamata was described from a single male collected by V. J. Tipton from a rodent nest in the Sierra Madre Occidental Range (Cerro Potosi) Nuevo León, Mexico, 20 April 1964, at an elevation of 3050 m. We have recently received several specimens referable to this species from the vicinity of Albuquerque, New Mexico. *Phalacropsylla* is redescribed to summarize the characteristics of this genus. Minor differences between the New Mexico males and the male holotype of *hamata* probably represent individual variation rather than subspecific differences (Fig. 3–5).

Phalacropsylla Rothschild 1915

Frontal tubercle and striarium absent. Eyes vestigial, eye spot lightly sclerotized. Genal comb of 2 overlapping teeth; outer tooth slightly over ½ length of narrower, subacute inner tooth. Pronotal comb of 14–18 spines. Abdominal spinelets and mesonotal pseudosetae present. Some subapical bristles of inner side of hind coxae weakly spiniform. Fifth segment of all tarsi with 4 lateral pair of bristles and 1 pair shifted to the plantar surface between the 1st lateral pair. Sternum of male V-shaped, distal arms bifid; distal arm with lightly sclerotized dorsal expansion and short, preapical spiniform bristles, plus long, curved, spiniform bristles in certain species.

Phalacropsylla hamata Tipton & Mendez

Phalacropsylla hamata Tipton & Mendez, 1968, Pac. Insects 10: 177–214.

Material.— All from Bernalillo Co., New Mexico, collected by Curt Montman. Allotype female ex *Peromyscus leucopus,* 20 November 1980. Parallotype female with same data. Male collections include 2 ex *P. leucopus* 20 November 1980, 1 ex *Neotoma albigula* 20 November 1980, and 1 ex *N. albigula* 20 February 1981. Allotype deposited in the United States National Museum of Natural History collection, Washington, D.C.

Diagnosis.— Flea specific differentiation in the absence of males is often difficult or impossible. In the *Phalacropsylla,* however, configuration of the caudal lobe of sternum VII seems to show sufficient distinctiveness to be of value in female specific identification. In *hamata, paradisea,* and *oregonensis* the female sternum caudal lobe is broader than long. The lobe is ca 3.5 × as broad as long in *hamata*, as opposed to less than 2 × as broad as long in *paradisea* and *oregonensis*. *Phalacropsylla* males are readily identified to species with the key presented by Lewis and Maser (1978).

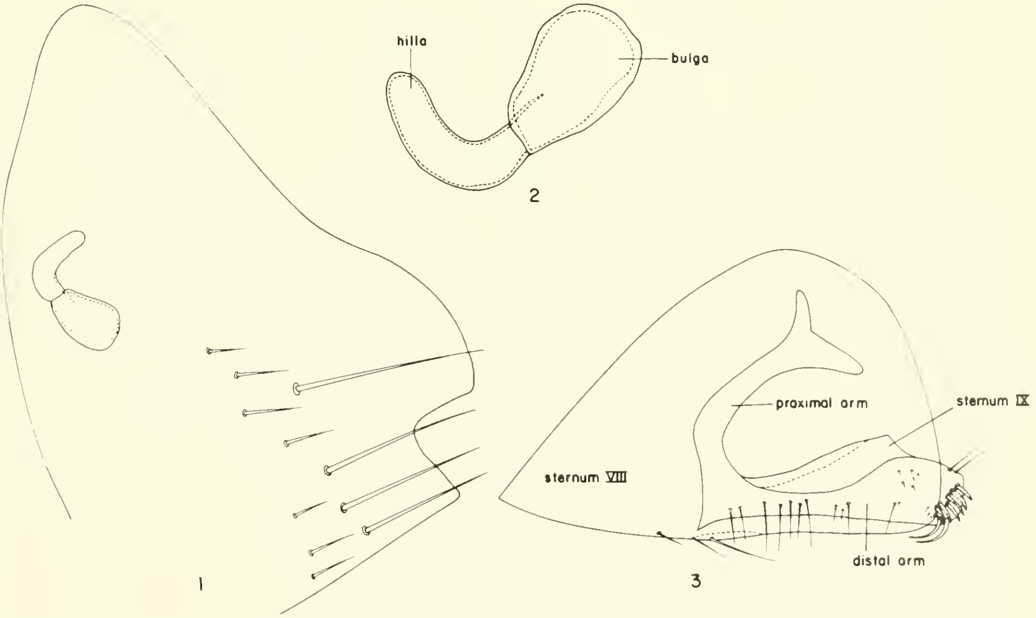
---

[1] Vector-Borne Viral Diseases Division, Center for Infectious Diseases, Centers for Disease Control, Public Health Service, U.S. Department of Health and Human Services, P.O. Box 2087, Fort Collins, Colorado 80522-2087.

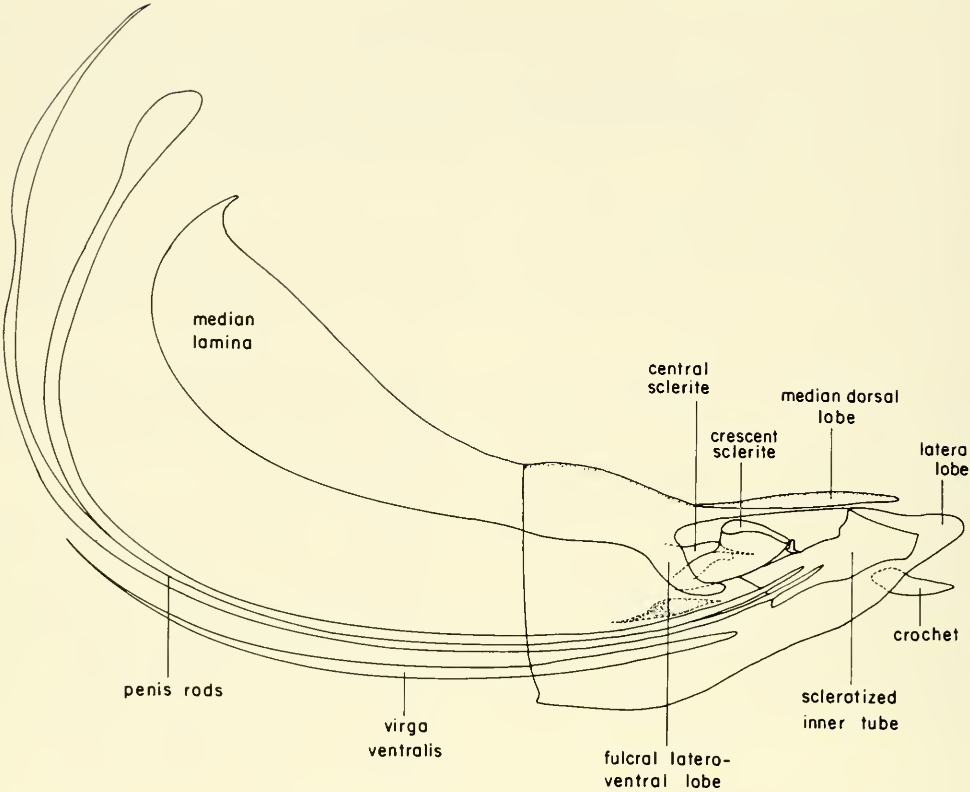
Description of female.— *Head*: Preantennal region with 2 fairly straight rows of bristles. Frontal row of 4 small, thin bristles; ocular row of 4 much larger ones and a fine bristle slightly out of line and cephalad of eye spot; 3 thin bristles caudad of ocular row. Maxilla narrow, acuminate distally, extending to base of 4th segment of maxillary palpus; maxillary palpus extending ca ⅔ length of coxa I. Labial palpus extending beyond apex of coxa I. Postantennal region with bristles arranged 1:3:5 on one side and 1:4:5 on the other, the caudal row with fine intercalaries; 18–20 fine hairs along the antennal fossa.

Thorax: Pronotum with a row of 6 large bristles, ventrad bristle 2 × length of others, separated by 5 smaller bristles per side; pronotal comb of 14 spines of ca same length, except for shorter ventralmost pair. Mesonotum with a row of 5 large bristles and fine intercalaries preceded by a row of 7 smaller ones and 15–18 fine bristles scattered along cephalad margin; mesonotal flange with 2 pseudosetae per side (parallotype with 3). Mesepisternum with a large, lateral bristle (parallotype with a fine bristle preceding large bristle on 1 side); mesepimeron with 2 irregular rows of bristles arranged 3:2 on one side and 4:2 on the other. Metanotum (exclusive of lateral metanotal area) with 3 rows of bristles, caudal row of 4–5 large ones and 5 fine intercalaries, a median row of 6 or 7 smaller bristles and a cephlad row of 2 or 3 still smaller bristles; a single fine bristle precedes the 3 rows; lateral metanotal area with 1 large dorsocaudal bristle, a large caudal bristle, and a fine ventral bristle. Metepisternum with 3 subdorsal bristles in a row, a large one flanked by 2 smaller ones; metepimeron with ca 6 lateral bristles arranged 3:3:1 (paratype 2:3:1).

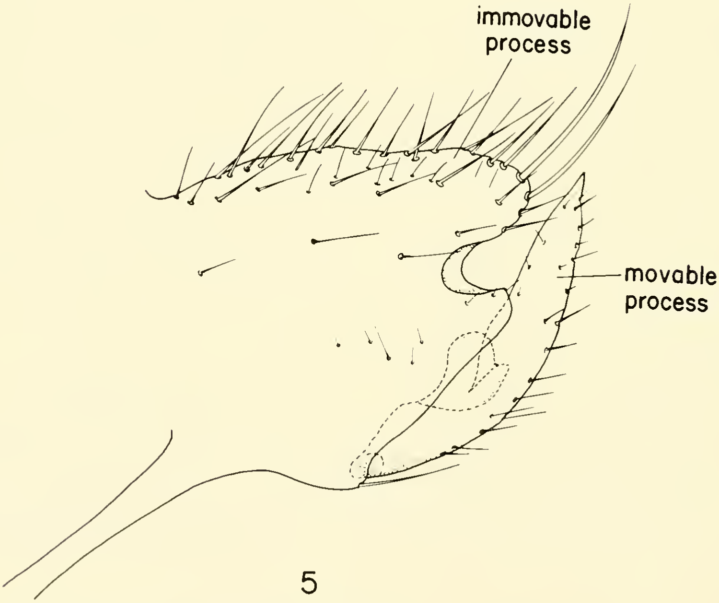
Abdomen: Terga I–IV with apical spinlets arranged (3-4), (4-4), (2-1), and (1-0), parallotype (3-3), (4-3), (3-3), and (1-1). Terga typically with median row of 5–7 large bristles alternating with smaller ones extending almost to ventral margin, preceded by a somewhat shorter row of 7 or 8 smaller bristles and 3 or 4 shorter bristles in an irregular row or patch on dorsocephalad margin. Middle antepygidial bristle ca 2 × length of ventral bristle and almost 3 × length of dorsal bristle. Sternum II with a vertical row of 3 large bristles, preceded by irregular row of 5



Figs. 1–3. *Phalacropsylla hamata*. 1, female sternum VII; 2, spermatheca; 3, male sterna VIII, IX.


median lamina
central sclerite
median dorsal lobe
crescent sclerite
lateral lobe
crochet
sclerotized inner tube
penis rods
virga ventralis
fulcral latero-ventral lobe

4


immovable process
movable process

5

Figs. 4,5. *Phalacropsylla hamata*. 4, male aedeagus; 5, male clasper.

or 6 smaller bristles and 3 or 4 small bristles toward ventral margin; other unmodified sterna with 4 large bristles preceded by 3 or 4 smaller ones.

Modified abdominal segments: (Fig. 1,2). Sternum VII with a large lobe on ventral half or caudal margin ca 3.5 × as broad as long; sinus directed cephalad, not forming definite ventral lobe. Sternum VII with subventral row of 4 (or 5) large bristles in a slightly oblique row, preceded by an irregular row of 7 or 8 smaller bristles. Spermatheca with bulga ca 1.5 × as broad as high; dorsal and ventral margins slightly concave at basal 3rd, becoming convex to form dilated, caudal ⅔ of bulga; hilla upcurved at basal 3rd, over 4 × as long as wide, about same width throughout, no constriction at basal 3rd. Tergum VIII with 2 irregular rows or 7 of 8 small, thin, bristles above the 8th spiracle; a curved row of 8–10 large bristles nearly sinuate, caudal margin, row beginning beneath ventral anal lobe and terminating just above ventral margin; 3–4 smaller, marginal bristles below ventral anal lobe, with 5–7 small, scattered, submedian bristles anterior to above fringe row.

DISCUSSION

The New Mexico *P. hamata* collection site was the rocky, lower slopes (1600–1800 m) of the Sandia Mountains, east of Albuquerque. These fleas were taken at elevations that include grassland communities grading into juniper (*Juniperus monosperma*)–pinyon (*Pinus edulis*) woodland. Hosts included *Peromyscus leucopus*, which lives among apache plume (*Fallugia paradoxa*) and saltbush (*Atriplex canescens*), and *Neotoma albigula*, which is found in both grassland and juniper-pinyon communities (Findley et al. 1975).

ACKNOWLEDGMENTS

We thank Dr. Robert Traub, University of Maryland, for comparing our material with the holotype of *P. hamata* in the U.S. National Museum collection. Mr. Curt Montman, Bernalillo County Department of Health, New Mexico, kindly provided the specimens.

Key to female *Phalacropsylla*

1.	Caudal lobe of st VII longer than broad	2
—	Caudal lobe of st VII broader than long	3
2(1).	Caudal lobe of st VII ca 1.5 × as long as broad	*nivalis*
—	Caudal lobe of st VII ca 1.9 × as long as broad	*allos*
3(1).	Caudal lobe of st VII 3.5 × as broad as long	*hamata*
—	Caudal lobe of st VII less than 2 × as broad as long	4
4(3).	Caudal lobe of st VII rectangular, broadly rounded at apex	*paradisea*
—	Caudal lobe of st VII more triangular, apex bluntly pointed and deflected ventrally	*oregonensis*

LITERATURE CITED

FINDLEY, J. S., A. H. HARRIS, D. E. WILSON, AND C. JONES. 1975. Mammals of New Mexico. Univ. of New Mexico Press, Albuquerque, New Mexico. 260 pp.

LEWIS, R. E., AND C. MASER. 1978. *Phalacropsylla oregonensis* sp. n., with a key to the species of *Phalacropsylla* Rothschild 1915 (Siphonaptera: Hystrichopsyllidae). J. Parasit. 64(1): 147–150.

TIPTON, V. J., AND E. MENDEZ. 1968. New species of fleas (Siphonaptera) from Cerro Potosi, Mexico, with notes on ecology and host parasite relationships. Pac. Insects 10(1): 177–214.

FIRST RECORD OF PYGMY RABBITS (*BRACHYLAGUS IDAHOENSIS*) IN WYOMING

Thomas M. Campbell III[1], Tim W. Clark[2], and Craig R. Groves[1]

Abstract.— Pygmy rabbits are reported for the first time in southwestern Wyoming. The range for this species is thus extended 240 km and 145 km from the nearest records in Idaho and Utah, respectively.

Although the pygmy rabbit occupies much of the sagebrush (*Artemisia tridentata*) habitat of the Great Basin, it has not been previously reported from Wyoming other than a single, unconfirmed observation described by Green and Flinders (1980a).

Between 11–20 October 1981, 6 specimens were collected (2 males, 4 females), 17 individuals were observed, and 2 skulls and numerous pellets were found at two sites in southwestern Wyoming. The first site was in South Fork Muddy Creek drainage, 8 km north and 8 km east of Carter, Uinta County, Wyoming (T17N R115W S4,5,6,33; T17N R116W S1,23, 24). The second site was along North Fork Muddy Creek drainage in Cumberland Flats, Lincoln and Uinta counties, Wyoming (T16N R118W S34; T19N R115W S19; T19N R116W S2,14). The two sites were geographically separated by the Hogsback and Oyster Ridge highlands.

The nearest previously reported records of pygmy rabbits are from the west near Pocatello, Bannock County, Idaho (Davis 1939), and near Clarkston, Cache County, Utah (Durrant 1952). These two new locales extend the known range of *B. idahoensis* approximately 240 km to the southeast and 145 km to the northeast, respectively. In view of the rough mountainous topography and the apparent lack of habitat between known range and this range extension, the pygmy rabbits in Wyoming may be a disjunct population.

Our observations at both sites showed *B. idahoensis* primarily confined to dense stands of big sagebrush growing in deep soils of drainages and hollows. This concurs with findings reported by Grinnell et al. (1930), Fisher (1979), and Green and Flinders (1980b). We also observed sign and collected two animals in a mixed sagebrush-greasewood (*Sarcobatus* spp.) habitat similar to that described by Davis (1939).

Mean external measurements of collected specimens were as follows:

Females (n = 4), total length, 265 mm; tail length, 23 mm; hind foot length, 78 mm; ear length, 53 mm.

Males (n = 2), total length, 238 mm; tail length, 21 mm; hind foot length, 77 mm; ear length, 55 mm.

The authors are presently engaged in a detailed study of distribution, habitat relationships, and taxonomic status of pygmy rabbits in Wyoming.

We acknowledge William Oelklaus for suggesting possible occurrence of this species in Cumberland Flats. Field assistance in an earlier unsuccessful attempt to document pygmy rabbit presence in Cumberland Flats was provided by Mark Stromberg and Howard Hunt. Denise Casey provided field assistance and critical review of the manuscript.

Literature Cited

Davis, W. B. 1939. The recent mammals of Idaho. Caxton Printers, Caldwell, Idaho. 400 pp.

Durrant, S. D. 1952. Mammals of Utah. Univ. of Kansas Publ. Mus. Nat. Hist. 6. 549 pp.

Fisher, J. W. 1979. Reproduction in the pygmy rabbit in southeastern Idaho. Unpublished thesis. Idaho State Univ., Pocatello. 32 pp.

Green, J. S., and J. T. Flinders. 1980a. *Brachylagus idahoensis*. Mammal. Species No. 125. Amer. Soc. of Mammal. 4 pp.

———. 1980b. Habitat and dietary relationships of the pygmy rabbit. J. Range Manage. 33:136–142.

Grinnell, J., J. Dixon, and J. M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. Univ. of California Pub. Zool. 35. 594 pp.

---

[1] Biota Research and Consulting, Inc., Box 2705, Jackson, Wyoming 83001.

[2] Department of Biology, Idaho State University, Pocatello, Idaho 83209.

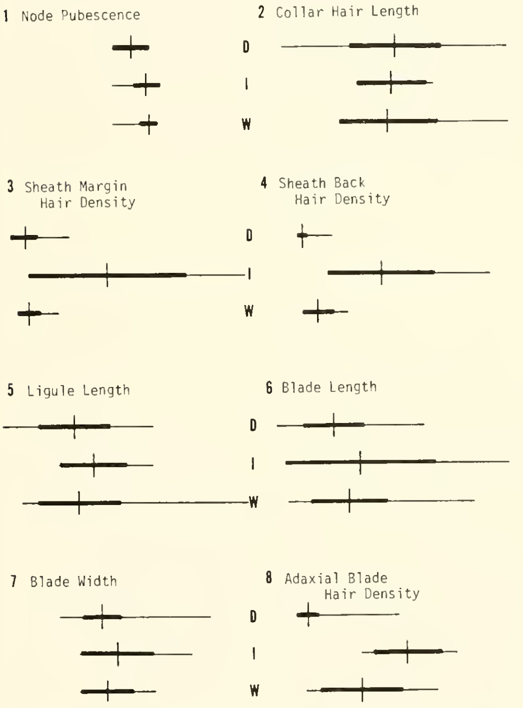
PASPALUM DISTICHUM L. VAR. *INDUTUM* SHINNERS (POACEAE)[1]

Kelly Wayne Allred[2]

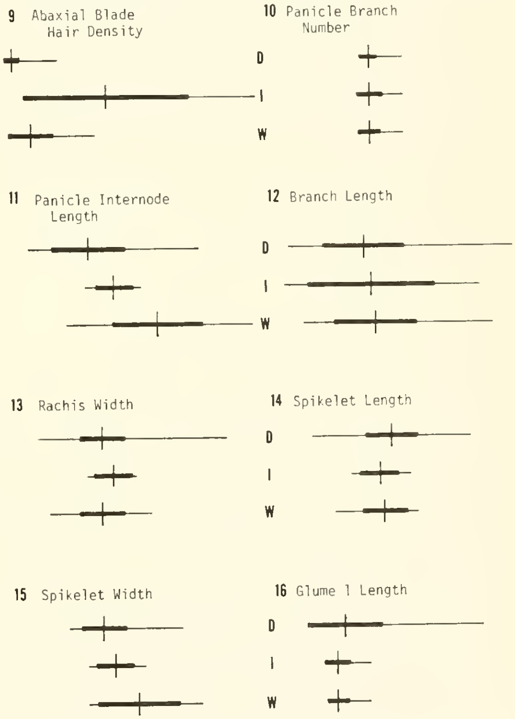
Abstract.— Glabrous *Paspalum distichum*, pubescent var. *indutum*, and pubescent plants of *P. distichum* from the western United States were compared. No morphological differences other than pubescence exist between the three forms. Plants from the eastern United States are generally more glabrous than those from western regions. The var. *indutum* represents an extreme pubescent form and is reduced to synonymy under *P. distichum*.

Paspalum distichum L.[3] is the familiar "knotgrass" of swamps, swales, marshes, ditches, and muddy sites throughout much of the continental United States. It grows along both eastern and western coasts and throughout the southern states. Knotgrass is also widespread in other warm-temperate to tropical regions of the world.

Material from Dallas County, Texas, with strongly hirsute sheaths and blades was



Figs. 1–8. Comparisons of the means (vertical line), range (horizontal line), and one standard deviation on each side of the mean (horizontal bar) for three forms of *Paspalum distichium*. D, glabrous *distichum* form; I, pubescent *indutum* form; W, pubescent western form. The features measured are as labeled.



Figs. 9–16. Comparisons of the means (vertical line), range (horizontal line), and one standard deviation on each side of the mean (horizontal bar) for three forms of *Paspalum distichum*. D, glabrous *distichum* form; I, pubescent *indutum* form; W, pubescent western form. The features measured are as labeled.

---

[1] Journal Article 903, Agricultural Experiment Station, New Mexico State University, Las Cruces, New Mexico 88003.

[2] Department of Animal and Range Sciences, New Mexico State University, Las Cruces, New Mexico 88003.

[3] There is current controversy concerning the application of this name, involving also the names *P. vaginatum* Sw. and *P. paspalodes* (Michx.) Scribner. Until this matter is resolved, I will use "*P. distichum*" in the sense of Hitchcock (1951). See also Guédès (1976) and Renvoize and Clayton (1980).

described by Shinners (1954) as *Paspalum distichum* var. *indutum*. The variety *indutum* has been known only from the type locality and a few collections in the same county. Many plants of *P. distichum* from the western United States, however, including the intermountain region, also possess varying degrees of pubescence on the sheaths and elsewhere. This fact suggested the following queries. How does the var. *indutum* compare with the typical glabrous material of var. *distichum*, and with the pubescent material of the western United States? Are there other features in addition to pubescence that serve to distinguish any of the three forms? What is the geographic distribution of these forms? How many taxa are involved in this complex?

MATERIALS AND METHODS

Plant specimens were gathered from various herbaria throughout the United States range of *Paspalum distichum* to give a representative sample of this taxon. From this sample, 235 specimens were examined and measurements taken for the following features: node pubescence, collar pubescence (length and number of hairs), sheath margin pubescence (density), sheath back pubescence (density), ligule length, blade length, blade width, adaxial blade pubescence (density), abaxial blade pubescence (density), number of inflorescence branches, length of the uppermost internode of the inflorescence, uppermost branch length, rachis width, spikelet length, spikelet width, and first glume length. Pubescence "density" was measured by the number of hairs touching or intersecting a standard 1 cm micrometer grid at 40X magnification. To help evaluate the relative degree of pubescence, a Pubescence Index (PI) was calculated for each specimen. The PI was the sum of the values for the pubescence features (node, collar, sheath margin, sheath back, adaxial blade, and abaxial blade). Totally glabrous plants would have a PI of zero,

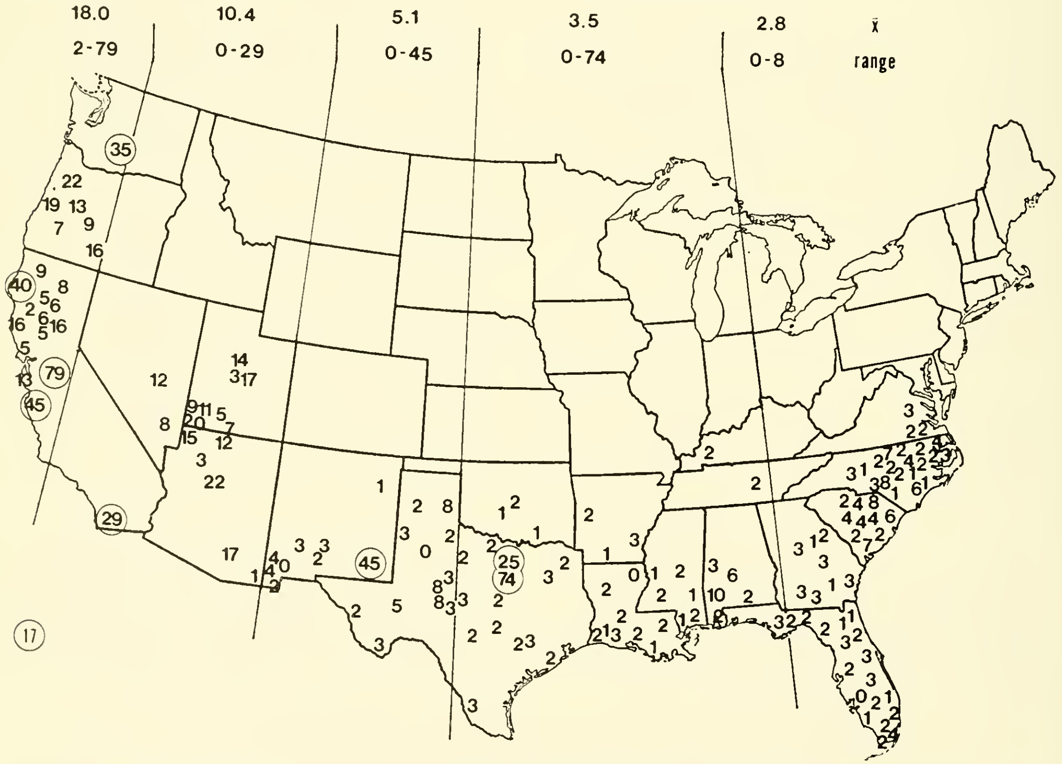


Fig. 17. Pubescence Index values of selected species of *Paspalum distichum* based on measurements of node pubescence, collar hair length, sheath margin hair density, sheath back hair density, adaxial blade hair density, and abaxial blade hair density. Circled PI values represent the *indutum* form. The map is not intended to represent the geographic distribution of *P. distichum*.

with greater PI values corresponding to increased pubescence.

RESULTS AND DISCUSSION

Most characteristics of *Paspalum distichum* are remarkably consistent throughout the continental United States. The three forms (glabrous *distichum*, *indutum*, and pubescent western) are essentially identical for all morphological features other than pubescence (Figs. 1–16). Even slight differences, such as the length of the panicle internode (Fig. 11) are not correlated with any other features. The obvious differences illustrated by Figures 1–16 are in the pubescence features, but these are the result of the a priori classification of the plants into three groups: glabrous *distichum*, pubescent *indutum*, and pubescent western forms.

The only possible differences, then, involve pubescence, which can be evaluated by the Pubescence Index (PI). The PI values for 161 specimens of knotgrass were plotted geographically (Fig. 17). (The remaining 74 specimens of the original 235 represented either duplicates or other specimens with identical PI values and from the same localities as those plotted on the map.) Specimens that were referable to the variety *indutum*, that is, with densely hirsute sheaths and blades as in the type specimen (*Shinners 10564*, SMU), were found in widely separate localities from Texas to Washington and had a PI range of 25–79. The type specimen of *indutum* had a PI value of 74.

There appears to be a rough cline in pubescence from more glabrous eastern plants (characteristic of *distichum*) to more pubescent western forms. Division of the United States into regions showed an average increase in PI values from 2.8 for eastern knotgrass to 18.0 for western plants (Fig. 17). The extreme pubescent forms representing variety *indutum* showed no such interrelationship with geographic distribution. High PI values

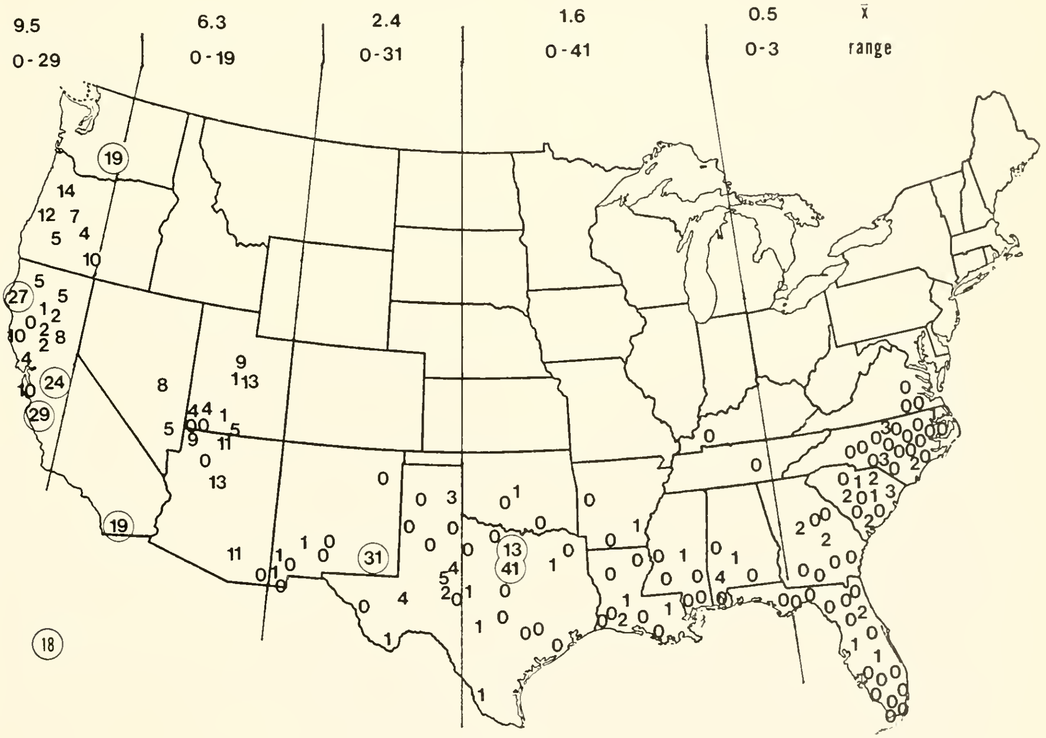


Fig. 18. Pubescence Index values of selected species of *Paspalum distichum* based on measurements of sheath back hair density, adaxial blade hair density, and abaxial blade hair density. Circled PI values represent the *indutum* form. The map is not intended to represent the geographic distribution of *P. distichum*.

(7–8) in eastern plants were due mainly to very pubescent nodes, collars, and sheath margins, but the pubescence of western plants involved not only the nodes, collars, and sheath margins, but also especially the sheath back and leaf blades. This is illustrated in Figure 18, where modified PI values from only the sheath back and blade surfaces are plotted. We see that eastern plants are glabrous or nearly so for these features (PI = 0.5), but western plants are often pubescent (PI = 9.5). The relationship, however, is far from absolute, as is shown by the range in PI for each region.

In conclusion, there is no morphological distinction between the nearly glabrous eastern knotgrass, the pubescent western forms, and the variety *indutum*. The variety *indutum* merely represents the extreme pubescent form of *Paspalum distichum*. Recognition of this taxon is untenable, with no basis in geographic distribution and no correlation with any other suite of features. The limits of such a taxon would be entirely arbitrary. Pubescence patterns in knotgrass do appear in an east-west continuum, but there is no strong geographic distinction nor any feature other than pubescence that would allow a taxonomic segregation. The variety *indutum* and other pubescent plants are best viewed as pubescent forms of *Paspalum distichum*.

Acknowledgments

Many thanks to the curators of the following herbaria for their generous loan of specimens: BRY, FSU, NCU, SMU, UNM, UTC, and WTU.

Literature Cited

Guédès, M. 1976. The case of *Paspalum distichum* and against futile name changes. Taxon 25(4):512.

Hitchcock, A. S. 1951. Manual of the grasses of the United States. USDA Misc. Publ. 200. 2d rev. ed. Agnes Chase.

Renvoize, S. A., and W. D. Clayton. 1980. Proposal to reject the name *Paspalum distichum* L. Taxon 29(¾):339–340.

Shinners, L. 1954. Notes on north Texas grasses. Rhodora 56:31–32.

LOCAL FLORAS OF THE SOUTHWEST, 1920–1980: AN ANNOTATED BIBLIOGRAPHY

Janice E. Bowers[1]

Abstract.— Local floras, that is, plant lists for relatively small areas, are widely scattered, often unpublished, and difficult to locate. Over 100 local floras from the southwestern United States (Arizona, Colorado, Nevada, New Mexico, and Utah) are listed and briefly annotated.

Much of the southwestern United States is well known botanically. Comprehensive, statewide floristic manuals have been prepared for Arizona (Tidestrom and Kittell 1941, Kearney and Peebles 1942, 1960), Colorado (Harrington 1954), New Mexico (Martin and Hutchins 1981), the Sonoran Desert (Shreve and Wiggins 1964), the Mojave Desert (Jaeger 1941), Utah (Welsh and Moore 1973), and the Intermountain Region (Holmgren and Reveal 1966, Tidestrom 1925, Cronquist et al. 1972, 1977). Floristic studies on a smaller scale have also contributed to knowledge about plant distribution in the Southwest, but these briefer works are often unpublished and difficult to locate. Botanical bibliographies such as those compiled by Ewan (1936) and Schmutz (1978) for Arizona, Hoffman and Tomlinson (1966) for Colorado, Christensen (1967a, 1967b) for Utah, and U.S. Fish and Wildlife Service (1977a, 1977b, 1977c) for Colorado, Utah, and New Mexico have not emphasized local floras.

The objective of this paper is to provide a list of readily accessible local floras for the Southwest, including Arizona, New Mexico, Utah, Nevada, and Colorado. Only plant lists intended to be more or less complete floras are included. Lists restricted to single life forms (such as cacti, woody plants, fungi, or ephemerals) are not included, nor are manuals that cover state-sized regions. Only the most recent flora for an area is listed. Both published and unpublished floras are included, with the reservation that unpublished lists must be readily accessible, either from the responsible agency or through the interlibrary loan programs of major universities. Floras published before 1920 are not included because they are seldom complete and can be difficult to locate. Arizona floras discussed by Bowers (1981) are included here as bibliographic citations only.

Arizona

Aitchison, S. W. 1978. Oak Creek Canyon and the red rock country of Arizona: a natural history and trail guide. Flagstaff, AZ: Stillwater Canyon Press.

Aitchison, S. W., and M. E. Theroux. 1974. A biotic inventory of Chevelon Canyon, Coconino and Navajo counties, Arizona. Flagstaff, AZ: U.S. Forest Service, Sitgreaves National Forest.

Bennett, P. S. 1978. Vascular plants, Grand Canyon National Park. Grand Canyon, AZ: Grand Canyon Computer Center. Available from Western Archaeological Center, 1415 N. 6th Ave., Tucson, AZ.

Bohrer, V. L., and M. Bergseng. 1963. An annotated catalogue of plants from Window Rock, Arizona. Window Rock, AZ: Navajo Tribal Museum.

Bowers, J. E. 1980. Flora of Organ Pipe Cactus National Monument. J. Arizona-Nevada Acad. Sci. 15:1–11, 33–47.

Brotherson, J. D., G. Nebeker, M. Skougard, and J. Fairchild. 1978. Plants of Navajo National Monument. Great Basin Nat. 38:19–30.

Burgess, R. L. 1965. A checklist of the vascular flora of Tonto National Monument. J. Arizona Acad. Sci. 3:213–223.

Butterwick, M., P. Fischer, D. Hillyard, and D. Ducote. 1980. Annotated checklist of vascular plants collected in the Harcuvar, Vulture and Skull Valley planning units. Phoenix, AZ: U.S. Dept. of the Interior, Bureau of Land Management. Available from Bureau of Land Management, Phoenix District Office, 2929 W. Clarendon Ave., Phoenix, AZ.

Butterwick, M., D. Hillyard, and B. Parfitt. 1979. Annotated list of taxa of vascular plants collected

---

[1] Office of Arid Lands Studies, University of Arizona, Tucson, Arizona 85721.

in the Hualapai-Aquarius environmental impact statement area. Phoenix, AZ: U.S. Dept. of the Interior, Bureau of Land Management. Available from Bureau of Land Management, Phoenix District Office, 2929 W. Clarendon Ave., Phoenix, AZ.

Fay, J. M. 1978. Vegetation and flora of the Patagonia-Sonoita Creek Sanctuary, Patagonia, Arizona. Tucson, AZ: Arizona Natural Heritage Program. Available from Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson, AZ.

Halse, R. R. 1973. The flora of Canyon de Chelly National Monument. Tucson, AZ: Univ. of Arizona. Unpublished thesis.

Hazen, J. M. 1978. The flora of Bill Williams Mountain. Flagstaff, AZ: Univ. of Northern Arizona. Unpublished thesis.

Holland, J. S., W. E. Niles, and P. J. Leary. Vascular plants of the Lake Mead National Recreation Area. Las Vegas, NV: Univ. of Nevada, Dept. of Biological Sciences. Lake Mead Tech. Rep. No. 3.

Joyce, J. F. 1976. Vegetational analysis of Walnut Canyon, Arizona. J. Arizona Acad. Sci. 11:127–135. Updates Spangle (1953).

Keil, D. J. 1973. Vegetation and flora of the White Tank Mountain Regional Park, Maricopa County, Arizona. J. Arizona Acad. Sci. 8:35–48.

Lane, M. A. 1981. Vegetation and flora of McDowell Mountain Regional Park, Maricopa County, Arizona. J. Arizona-Nevada Acad. Sci. 16:29–38.

Lehto, E. 1970. A floristic study of Lake Pleasant Regional Park, Maricopa County, Arizona. Tempe, AZ: Arizona State Univ. Unpublished thesis.

Leithliter, J. R. 1980. Vegetation and flora of the Chiricahua Wilderness Area. Tempe, AZ: Arizona State Univ. Unpublished thesis. Lists 300 taxa for 72.8 km^2. Reviews history of the area; describes topography, geology, soils and climate. Compares vegetation of study area to that of nearby mountain ranges. Annotations of the plant list include synonymy, common names, relative abundance, vegetation type, habitat, elevational range, phenology, and collection numbers. Provides small-scale topographic and geologic maps.

McCulloch, C. Y., and C. P. Pase. 1968. Pages 77–88 *in* Checklist of plants of the Three Bar Wildlife Area. Arizona Game and Fish Dept. Wildlife Research in Arizona 1967. Phoenix, AZ: Arizona Game and Fish Dept.

McDougall, W. B. 1959. Typical seed plants of the ponderosa pine zone. Flagstaff, AZ: Museum of Northern Arizona. Bulletin No. 32.

———. 1959. Plants of the Glen Canyon area in the herbarium of the Museum of Northern Arizona. Flagstaff, AZ: Museum of Northern Arizona. Available from Museum of Northern Arizona, Flagstaff, AZ.

McDougall, W. B. 1962. Seed plants of Wupatki and Sunset Crater National Monuments. Flagstaff, AZ: Museum of Northern Arizona. Bulletin No. 37.

McDougall, W. B., and H. S. Haskell. 1960. Seed plants of Montezuma Castle National Monument. Flagstaff, AZ: Museum of Northern Arizona. Bulletin No. 35.

McGill, L. A. 1979. Vascular flora. Pages 56–83 *in* W. L. Minckley; Sommerfeld, M. R., eds., Resource inventory for the Gila River Complex, eastern Arizona. Safford, AZ: U.S. Dept. of the Interior, Bureau of Land Management. Available from Bureau of Land Management, Safford District Office, 425 E. 4th St., Safford, AZ.

McLaughlin, S. P. 1978. Productivity of the understory community in an Arizona ponderosa pine forest. Tucson, AZ: Univ. of Arizona. Unpublished dissertation.

McLaughlin. S. P., and W. Van Asdall. 1977. Flora and vegetation of the Rosemont area. Pages 64–98 *in* R. Davis, and J. R. Calahan, eds., An environmental inventory of the Rosemont area in southern Arizona. Vol. 1. Tucson, AZ: Univ. of Arizona. Deposited at Univ. of Arizona, Science Library, Tucson, AZ.

Pase, C. P., and R. R. Johnson. 1968. Flora and vegetation of the Sierra Ancha Experimental Forest, Arizona. Fort Collins, CO: U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station. Research Paper No. 41.

Paulik, L. A. 1979. A vascular flora of the subalpine spruce-fir forest of the San Francisco Peaks, Arizona. Flagstaff, AZ: Northern Arizona Univ. Unpublished thesis.

Petrified Forest National Park. 1976. Seed plant checklist of Petrified Forest National Park. Available from Petrified Forest National Park, Arizona 86028.

Phillips, A. M. III. 1975. Flora of the Rampart Cave area, lower Grand Canyon, Arizona. J. Arizona Acad. Sci. 10:148–159.

Pierce, A. L. 1979. Vegetation and flora of Buckeye Hills Recreation Area, Maricopa County, Arizona. Tempe, AZ: Arizona State Univ. Unpublished thesis. Lists 175 taxa for 1500 ha. Reviews history of the area; describes climate, topography, geology, and soils. Discusses vegetation, listing important species for each plant community. Compares flora to that of six other regional parks in Maricopa County. Annotations of the plant list include plant community, relative abundance, and regional distribution. Provides soil and topographic maps, photographs of plant communities.

Reeves, T. 1976. Vegetation and flora of Chiricahua National Monument, Cochise County, Arizona. Tempe, AZ: Arizona State Univ. Unpublished thesis.

Schaak, C. G. 1970. A flora of the arctic-alpine vascular plants of the San Francisco Mountain, Arizona. Flagstaff, AZ: Northern Arizona Univ. Unpublished thesis.

Schilling, M. A. 1980. A vegetational survey of the Volunteer and Sycamore Canyon region. Flagstaff, AZ: Northern Arizona Univ. Unpublished thesis. Volunteer and Sycamore Canyons are located in southern Coconino County.

Schmutz, E. M., C. C. Michaels, and B. I. Judd. 1967. Boysag Point: a relict area on the North Rim of the Grand Canyon in Arizona. J. Range Manage. 20:363–369.

Simmons, N. M. 1966. Flora of the Cabeza Prieta Game Range. J. Arizona Acad. Sci. 4:93–104.

Smith, E. L. 1974. Phelps Cabin Research Natural Area. Pages 127–133 *in* E. L. Smith, Established natural areas in Arizona: a guidebook for scientists and educators. Phoenix, AZ: Office of Economic Planning and Development.

Spangle, P. F. 1953. A revised checklist of the flora of Walnut Canyon National Monument. Plateau 26:86–88.

Sundell, E. G. 1974. Vegetation and flora of the Sierra Estrella Regional Park, Maricopa County, Arizona. Tempe, AZ: Arizona State Univ. Unpublished thesis.

Toolin, L. J. 1979. A floral survey of Thomas Canyon, Baboquivari Mountains, Pima County, Arizona. Tucson, AZ: Arizona Natural Heritage Program. Available from Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson, AZ.

———. 1980. Final report on the flora of Ramsey Canyon. Tucson, AZ: Arizona Natural Heritage Program. Available from Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson, AZ. Ramsey Canyon is in the Huachuca Mountains, Cochise County.

Toolin, L., T. R. Van Devender, and J. M. Kaiser. 1980. The flora of Sycamore Canyon, Pajarito Mountains, Santa Cruz County, Arizona. J. Arizona-Nevada Acad. Sci. 14:66–74.

Turner, R. M. 1977. Plant species list: Tumamoc Hill. Tucson, AZ: U.S. Geological Survey. Available from USGS Research Project Office, 301 W. Congress, Tucson, AZ. Tumamoc Hill is in the Tucson Mountains, Pima County.

Wadleigh, R. 1969. Plant list for Tucson Mountain District of Saguaro National Monument. Tucson, AZ: Saguaro National Monument. Available from Saguaro National Monument, Rt. 9, Box 595, Tucson, AZ.

Warren, P. L., and L. S. Anderson. 1980. Annotated checklist of plants of the George Whittell Wildlife Preserve. Pages 80–124 *in* T. B. Johnson, ed., 1980 progress report for the biological survey of the George Whittell Wildlife Preserve, Graham and Pinal counties, Arizona. Tucson, AZ: Arizona Natural Heritage Program. Available from Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson, AZ.

Welsh, S. L., N. D. Atwood, and J. R. Murdock. Kaiparowits flora. Great Basin Nat. 38:125–179.

Yatskievych, G. A. 1980. Plant list for O'Donnell Canyon, Canelo Hills, Santa Cruz County, Arizona. Tucson, AZ: Arizona Natural Heritage Program. Available from Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson, AZ.

Yatskievych, G. A., and C. E. Jenkins. 1981. Fall vegetation and zonation of Hooker Cienega, Graham County, Arizona. J. Arizona-Nevada Acad. Sci. 16:7–11.

Colorado

Barrell, J. 1969. Flora of the Gunnison Basin, Gunnison, Saguache, and Hinsdale counties, Colorado: a study in the distribution of plants. Lists 1062 taxa. Annotated with detailed distributional information. Includes glossary of botanical terms. *Fide* Donald J. Pinkava, Arizona State Univ.

Bradley, R. A. W. 1950. The vascular flora of Moffat County, Colorado. Boulder, CO: Univ. of Colorado. Thesis. Lists 511 taxa for 1,231,606 ha; annotations of the plant list include collector, collection location and number, elevation, and habitat. Describes topography, history of plant collection; discusses vegetation zones. Lists plants occurring in Colorado only in Moffat County. Includes location map of study area and photos of vegetation types.

Colorado National Monument. 1980. Plants recorded from Colorado National Monument. Fruita, CO: Colorado National Monument. Available from Colorado National Monument, Fruita, CO. Lists 347 taxa for 8276 ha; plant list annotated with common names.

Cox, C. F. 1933. Alpine plant succession on James Peak, Colorado. Ecol. Monographs 3:299–372. Lists 292 taxa. Discusses geology and physiography, climate, effects of grazing and fire, and history of botanical collection. Describes plant communities, with species lists for each. Discusses endemic and disjunct species, floristic affinities of the flora, and ecology of alpine plants.

Hlina, P. 1980. Preliminary list of vascular plants, Great Sand Dunes National Monument. Alamosa, CO: Great Sand Dunes National Monument. Available from Great Sand Dunes National Monument, Box 60, Alamosa, CO. Lists 252 taxa for 15,764 ha; plant list annotated with common names.

Holm, T. H. 1923. The vegetation of the alpine region of the Rocky Mountains in Colorado. Mem. Nat. Acad. Sci. 19:1–45. Lists 170 taxa; annotations of plant list include relative abundance, habitat, elevation, and collection localities. Discusses geographical distribution of the species, origins of the flora, vegetation zones. Provides location map.

Langenheim, J. H. 1955. Flora of the Crested Butte Quadrangle, Colorado. Madroño 13:64–78. Lists 579 taxa for 25,907 ha; annotations of plant list include collection numbers and species collected outside the study area. Discusses geographical affinities of the flora and describes vegetation zones.

Litzinger, W. 1976. Annotated checklist of vascular plants of Cajon Mesa, Colorado-Utah. Pages 387–432 *in* J. C. Winter, ed., Hovenweep 1975. San Jose, CA: San Jose State Univ. Archaeological Report No. 2. Lists 258 taxa. The study area includes Hovenweep National Monument. Annotations include common names, habit, local distribution, habitat, phenology, and relative abundance.

McNeal, D. W. 1976. Annotated checklist of the alpine vascular plants of Specimen Mountain, Rocky Mountain National Park, Colorado. Southwestern Naturalist 20:423–435. Lists 178 taxa; annotations of the plant list include relative abundance, collection numbers, habitat, elevational range, and phenology. Discusses topography, climate; describes alpine habitats.

Nelson, R. A. 1976. Plants of Rocky Mountain National Park. Washington, D.C.: Government Printing Office. Available from Rocky Mountain National Park, Estes Park, CO. Lists 850 taxa; annotations include common names, species descriptions, habitat, local distribution, elevational range, ethnobotanical notes. Provides keys to species and many photographs of plants and habitats. Includes location map and glossary of botanical terms.

Vories, K. C. 1974. A vegetation inventory and analysis of the Piceance Basin and adjacent drainages. Gunnison, CO: Western State College of Colorado. Unpublished thesis. Lists 413 taxa for 416,000 ha; annotations of plant list include local distribution, common names, habit, nativity, rare or endangered status. Discusses physiography, climate, and land use. Quantitative analysis of plan tcommunities is discussed in detail. Provides small-scale vegetation maps, many photographs of plant communities.

Welsh, S. L., and J. A. Erdman. 1964. Annotated checklist of the plants of Mesa Verde, Colorado. Brigham Young Univ. Sci. Bull., Bio. Ser. 4(2):1–32. Lists 411 taxa for 51,813 ha; annotations of the plant list include collection location and number, collector, common names, relative abundance, habitat, local distribution, phenology, and plants found in prehistoric ruins. Briefly discusses topography and history of plant collection.

Weber, W. A. 1976. Rocky Mountain flora. 5th ed. Boulder, CO: Univ. of Colorado Press. Lists 1600 taxa; annotations include common names, relative abundance, habit, and brief species descriptions. Reviews botanical collection; describes plant communities; discusses plant geography of the Rocky Mountains. Provides keys to species, glossary of botanical terms; includes small-scale location map and photographs and line drawings of many species.

NEVADA

Beatley, J. C. 1976. Vascular plants of the Nevada Test Site and central-southern Nevada: ecologic and geographic distributions. Springfield, VA: National Technical Information Center. Lists 1093 taxa for 24,500 km^2; annotations include relative abundance, habitat, plant community, common names, local distribution, elevational range, habit, and phenology. Discusses history of botanical collection; describes physiography, geology, soils, and climate. Describes plant communities, listing dominants. Correlates plant communities with topography and environmental variables. Includes many photographs of plant communities, small-scale maps showing physiographic and political features and vegetation types.

Bell, K. L., and R. E. Johnson. 1980. Alpine flora of the Wassuk Range, Mineral County, Nevada. Madroño 27:25–35. Lists 70 taxa for 260 ha; annotations of plant list include habitat, relative abundance, and regional distribution. Discusses geology, defines alpine zone. Discusses endemism and species diversity, compares flora to that of other Great Basin alpine regions. Analyzes geographic affinities of the flora.

Bradley, W. G. 1967. A geographical analysis of the flora of Clark County, Nevada. J. Arizona Acad. Sci. 4:151–162. Lists 887 taxa. Discusses geographical affinities and origins of the flora.

Clokey, I. 1951. Flora of the Charleston Mountains, Clark County, Nevada. Berkeley, CA: Univ. of California Press. Lists 699 taxa for 170,000 ha; annotations include habitat, associated species, phenology, local distribution, geographical range, elevational range, collector and collection number, synonymy, type locality. Describes botanical collection, geology, climate; discusses endemism, geographical affinities of the flora. Contains keys to species.

Freeman, J., and J. L. Mahoney. 1977. Geothermal areas in Nevada: the distribution of vascular plants near the thermal springs surveyed. Mentzelia 3:8–14. Lists 125 taxa; annotations of plant list include collection locations, relative abundance. Includes small-scale location map.

Holmgren, A. H. 1942. Handbook of the vascular plants of northeastern Nevada. Logan, UT: Utah State Agricultural College. Lists 1205 taxa; annotations include common names, forage value, local and regional distribution, habitat, relative abundance, synonymy, and elevational range. Discusses botanical exploration, climate, physiography. Includes keys to species.

Lewis, M. C. 1976. Flora of Santa Rosa Mountains. Ogden, Utah: U.S. Forest Service. Available from Intermountain Region, U.S. Forest Service, Ogden, UT. Lists 347 taxa; annotations of plant list include plant community and collection location. Describes plant communities.

Linsdale, M. A., J. T. Howell, and J. M. Linsdale. 1952. Plants of the Toiyabe Mountains area, Nevada. Wasmann J. Bio. 10:129–200. Lists 521 taxa; annotations of plant list include collection date, location, and number, geographic range, and elevation. Discusses climate, distribution of some major shrub and tree species, geographic affinities of the flora. Compares flora to that of the Charleston Mountains. Includes photographs of plant communities, location map.

NEW MEXICO

Bedker, E. J. 1966. A study of the flora of the Manzano Mountains. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 396 taxa; plant list annotated with collection locations. Discusses topography, climate, geology, soils and life zones; describes 17 study sites in the Manzano Mountains in terms of location, geological features, soils, plant communities, and dominant species. Provides keys to species, location map, and photographs of plant communities. Compares flora to that of Mount Taylor, discusses species distribution in relation to environmental factors.

Campbell, R. S., and I. F. Campbell. 1938. Vegetation on gypsum soils of the Jornada Plain, New Mexico. Ecology 19:572–577. Lists 8 taxa based on 10 years of observation and collection. Discusses climate, soil chemistry, and soil physical properties in relation to the depauperate flora and sparse vegetation.

Capulin Mountain National Monument. 1980. Plant checklist: Capulin Mountain National Monument, New Mexico. Capulin, NM: Capulin Mountain National Monument. Available from Capulin Mountain National Monument, Capulin, NM. Lists 172 taxa for 310 ha; plant list annotated with common names.

Chaco Canyon National Monument. 1979. Checklist of plants for Chaco Canyon National Monument, New Mexico. Bloomfield, NM: Chaco Canyon National Monument. Available from Chaco Culture National Historical Park, Star Rt. 4, Box 6500, Bloomfield, NM. Lists 247 taxa for 8705 ha; plant list annotated with common names and introduced species. The list is currently being updated by Anne Cully.

Fletcher, R. A. 1972. A floristic assessment of the Datil Mountains. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 590 taxa for 82,902 ha; annotations include common names, phenology, elevational range, parent material, life form, relative abundance, geographical range, forage value, poisonous properties, and taxonomic comments. Lists noteworthy collections, major collection sites, and birds and mammals observed in the area. Discusses land use, topography, geology, soils, and climate. Describes plant associations. Analyzes geographic affinities of the flora, compares flora to those of neighboring states, compares affinities and species richness of floras on different substrates.

Fosberg, F. R. 1940. The aestival flora of the Mesilla Valley region, New Mexico. American Midland Naturalist 23:573–593. Lists 504 taxa; annotations of plant list include plant community and habitat. Describes plant communities and habitat; discusses topography and climate. Includes small-scale vegetation map.

Gehlbach, F. R., B. H. Warnock, W. C. Martin, and H. K. Sharsmith. 1969. Vascular plants of Carlsbad Caverns National Park, New Mexico, and adjacent Guadalupe Mountains (New Mexico–Texas). Carlsbad, NM: Carlsbad Caverns National Park. Available from Carlsbad Caverns National Park, NM. Lists 640 taxa for 18,921 ha; annotations of plant list include common names, habit, and phenology.

Hall, H. H., and S. Flowers. 1961. Vascular plants found in the Navajo Reservoir Basin, 1960, Colorado and New Mexico. Pages 47–90 *in* A. M. Woodbury, ed., Ecological studies of the flora and fauna of Navajo Reservoir, Colorado and New Mexico. Salt Lake City, UT: Univ. of Utah. Anthropological Paper No. 55. Lists 287 taxa for 6880 ha; annotations include common names, elevation, relative abundance, collector, and collection location and date.

Hutchins, C. R. 1974. A flora of the White Mountains area, southern Lincoln and northern Otero counties, New Mexico. Albuquerque, NM: C. R. Hutchins. Lists 1686 taxa; location map provided; annotations include synonymy, phenology, species descriptions, elevational range, habitat, and common names. Provides keys to species and glossary of botanical terms. Discusses topography and climate. Lists subalpine taxa.

Little, E. L., Jr., and R. S. Campbell. 1943. Flora of Jornada Experimental Range, New Mexico. Amer. Midl. Naturalist 30:626–670. Lists 528 taxa for 78,265 ha; annotations include geographic range of species, Raunkaier life form. Discusses history of botanical collection, geographic affinities of flora, distinctive species. Compares floristic composition and plant cover of the Jornada plain with nearby mountain meadows; discusses forage value of various species. Lists weeds. Provides location map and photographs of vegetation types and plants.

Mackay, H. A. 1970. A comparative floristic study of the Rio Hondo Canyon-Lake Fork-Wheeler Peak locale, New Mexico, and the Huerfano River-Blanco Peak locale, Colorado. Albuquerque, NM: Univ. of New Mexico. Unpublished dissertation. Lists 359 taxa for Rio Hondo locale, 467 taxa for Huerfano River locale; annotated with elevational ranges of each species. Discusses floristic differences between the two locales and describes vegetation zones. Collection sites are described in terms of topographic location, elevational range, and characteristic species. Describes geology and topography. Provides keys to species, vegetation maps at 1:63,000, photographs of vegetation types.

Manthey, G. T. 1977. A floristic analysis of the Sevilleta Wildlife Refuge and the Ladron Mountains. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 728 taxa. Annotations of plant list include plant community, common name, phenology, and elevational range. Describes topography, geology, climate, soils, and land use. Discusses floristic affinities, community integrity of plant communities, geographic patterns of each community. Describes plant communities, listing major and common species, habitat, elevational range, and local distribution of each. Lists taxa which terminate their distribution in or near the study area. Includes keys to species and a topographic map of the study area.

Martin, W. C., C. R. Hutchins, and R. G. Woodmansee. 1971. A flora of the Sandia Mountains, New Mexico. Albuquerque, NM: Sandia Press. Lists 884 taxa; annotations include species descriptions, elevational range, common names, and synonymy. Includes keys to species and glossary of botanical terms. Discusses geology, vegetation zones, and climate.

Martin, W. C., and W. L. Wagner. 1974. Biological survey of Kirtland Air Force Base (East) [Microform]. Washington, D.C.: Government Printing Office; SAND-74-0393. Available from National Technical Information Service, Springfield, VA.

Lists 369 taxa for 19,430 ha; annotated with common names, habitat, plant community. Describes topography, soils, climate; discusses biogeographical influences and disturbance patterns. Describes plant communities. Includes checklists of amphibians, reptiles, mammals, and birds.

OSBORN, N. L. 1962. The flora of Mount Taylor. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 301 taxa; includes keys to species. Discusses life zones; describes collection sites in terms of geographic location, elevation, life zone, geological features, dominant species. Includes checklist of all species collected at each site. Compares flora to that of other mountain ranges.

———. 1966. A comparative floristic study of Mount Taylor and Redondo Peak, New Mexico. Albuquerque, NM: Univ. of New Mexico. Unpublished dissertation. Lists 231 taxa for Redondo Peak. Describes life zones, collection locations. Compares floras of the two peaks, listing species found on both. Compares populations of three species found on both peaks to detect possible evolutionary trends. Reviews paleobotany of the region. Includes keys to species.

RIFFLE, N. L. 1973. The flora of Mount Sedgwick and vicinity. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 353 taxa; plant list annotated with collection locations. Briefly discusses geology and climate. Describes habitats of collection locations and lists dominant and interesting plants of each.

ROBERTSON, C. W. 1968. A study of the flora of Cochiti and Bland canyons of the Jemez Mountains. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 373 taxa. Discusses topography, soils, geology, and climate. Describes plant communities of each elevational zone. Compares floras of Cochiti and Bland canyons. Provides keys to species; includes topographic map and photographs of topography and vegetation. Plant checklist is annotated with collection locations.

SCHAFFNER, E. R. 1948. Flora of the White Sands National Monument of New Mexico. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 110 taxa for 56,757 ha; annotations include common names, local distribution, relative abundance, ethnobotanical notes, palatability for livestock, synonymy, and identification notes. Includes keys to species, photographs of vegetation, and topography. Discusses geology, topography, climate, collection history, and adaptation of plants to dunes. Lists gypsum indicator plants.

TATSCHL, A. K. 1966. A floristic study of the San Pedro Parks Wild Area, Rio Arriba County, New Mexico. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 288 taxa. Briefly describes topography, soils, and climate. Discusses life zones, lists representative species. Describes nine major collecting locations in terms of elevational range, dominant plants, habitat. Provides keys to species. Includes location and physiographic maps, photographs of plant communities. Plant checklist annotated with collection locations.

VAN DEVENDER, T. R., AND B. L. EVERITT. 1977. The latest Pleistocene and Recent vegetation of the Bishop's Cap, south central New Mexico. Southwestern Naturalist 22:337–352. Lists 118 taxa. Discusses climate, packrat ecology, modern and fossil floras in relation to climatic change. Lists 39 plant species found as macrofossils in packrat middens dating from 10,500 B.P.

WAGNER, W. L. 1973. Floristic affinities of Animas Mountain, southwestern New Mexico. Albuquerque, NM: Univ. of New Mexico. Unpublished thesis. Lists 718 taxa for 96,000 ha; annotations of plant list include life form, habitat, relative abundance, geographic range, plant community, synonymy, taxonomic comments and endemic species. Describes climate and topography. Discusses factors in plant distribution and dispersal, evolution of the flora, and distributional patterns of the various life forms. Defines Northern Sierra Madre Biotic Province, analyzes geographic affinities of the flora and the plant communities. Describes collection sites and plant communities in terms of dominant perennials and characteristic annuals, elevational range, ecological factors and topographic location.

WYNHOFF, J. T., E. LEHTO, AND D. J. PINKAVA. 1976. Vegetation of Cutler Canyon and vicinity, San Juan County, New Mexico. Washington, D.C.: U.S. Dept. of the Interior, Bureau of Land Management. Lists 436 taxa; annotations include relative abundance, common name, habitat. Includes photographs of habitat. *Fide* Donald J. Pinkava, Arizona State University.

UTAH

ALLRED, K. W. 1975. Timpanogos flora. Provo, UT: Brigham Young Univ. Thesis. Lists 684 taxa for 15,544 ha; annotations of plant list include habitat, phenology, elevational range, and collector and collection number. Discusses history of botanical collection. Describes topography, climate, vegetation zones. Lists dominant and characteristic species of each vegetation zone. Includes keys to species.

ARNOW, L. A. 1971. Vascular flora of Red Butte Canyon, Salt Lake County, Utah. Salt Lake City, UT: Univ. of Utah. Unpublished thesis. Lists 511 taxa for 2228 ha; annotations include species descriptions, common names, phenology, habitat, taxonomic comments, and plant associations. Briefly discusses topography, climate, geology, and history of botanical collection. Includes keys to species and glossary of botanical terms.

ARNOW, L. A., B. J. ALBEE, AND A. M. WYCKOFF. 1980. Flora of the central Wasatch Front, Utah. Salt Lake City, UT: Univ. of Utah Printing Service. Available from Univ. of Utah Bookstore, Salt Lake City, UT. Lists 1139 taxa for 260,000 ha. Briefly discusses vegetation of elevational zones, climate, and topography. Annotations include synonymy, common names, species descriptions, phenology, habitat, and elevational range. Provides keys to species and an illustrated glossary of botanical terms.

Buchanan, H., and G. T. Nebeker. 1971. Checklist of the higher plants of Bryce Canyon National Park, Utah. Ogden, UT: Weber State College Printing Dept. Lists 324 taxa. Describes and illustrates habitats of Bryce Canyon. Plant list annotated with common names. *Fide* Donald J. Pinkava, Arizona State University.

Castle, E. D. 1954. The succession of vegetation on a southern Utah sand dune. Provo, UT: Brigham Young Univ. Unpublished thesis. Lists 65 taxa; annotations of plant list include plants collected near the dunes. Discusses physiography, climate, and dune plant morphology. Describes vegetation on active and stable dunes. Discusses plant succession, limiting factors for plants on sand. Includes photographs of vegetation and topography.

Flowers, S., H. H. Hall, and G. T. Groves. 1959. Annotated list of plants found in Flaming Gorge Reservoir Basin. Pages 49–98 *in* A. M. Woodbury, ed., Ecological studies of the flora and fauna of Flaming Gorge Reservoir Basin, Utah and Wyoming. Salt Lake City, UT: Univ. of Utah; 1960. Anthropological Paper No. 48. Lists 448 taxa for river length of 142 km; annotations include relative abundance, habitat, elevational range, collection locations, and collector.

Graham, E. H. 1937. Botanical studies in the Uinta Basin of Utah and Colorado. Annals of the Carnegie Museum, Pittsburgh 26. Lists 1104 taxa for 3,108,808 ha; annotations include common names, relative abundance, habitat, collection location, elevation, vegetation zone, phenology and collector, collection date and number. Discusses history of exploration and settlement in Utah, history of botanical collection. Describes topography, climate, geology; vegetation zones, comparing them with those of surrounding areas; plant communities, listing dominant and secondary species of each. Eighty-nine collection locations are described in terms of location, plant community, elevation, and substrate. Discusses geographic affinities of flora; lists range extensions, new varieties, and species.

Harrison, B. F., S. L. Welsh, and G. Moore. 1964. Plants of Arches National Monument. Brigham Young Univ. Sci. Bull., Biol. Ser. 5(1):1–23. Lists 322 taxa for 29,696 ha; annotations include collection location and collector, relative abundance, habitat, local distribution, and common names. Briefly discusses climate, geology, and habitat. Lists endemics, discusses introduced species.

Higgins, L. C. 1967. A flora of the Beaver Dam Mountains. Provo, UT: Brigham Young Univ. Unpublished thesis. Lists 667 taxa; annotations of plant list include geographic range, relative abundance, elevational range, collector, and collection number. Briefly describes geology, major plant communities, topography. Discusses history of botanical collection. Includes keys to species. Lists range extensions, endemic species.

Holmgren, A. H. 1948. Handbook of the vascular plants of the northern Wasatch. 3d ed. Palo Alto, CA: National Press. Lists 1266 taxa, including many cultivated plants. Annotations include common names, habitat, local distribution, synonymy. Includes keys to species and glossary of botanical terms.

Lewis, M. E. 1973. Wheeler Peak area species list. Ogden, UT: U.S. Forest Service. Available from Intermountain Region, U.S. Forest Service, Ogden, UT. Lists 409 taxa; annotations of plant list include plant community, habitat, and relative abundance.

McMillan, C. 1948. A taxonomic and ecological study of the flora of the Deep Creek Mountains of central western Utah. Salt Lake City, UT: Univ. of Utah. Unpublished thesis. Lists 431 taxa; annotations of plant list include relative abundance, local distribution, and habitat. Describes physiography, climate, vegetation zones. Discusses history of botanical collection, effects of glaciation, phytogeography. Includes photographs of vegetation types.

Meyer, S. E. 1976. Annotated checklist of the vascular plants of Washington County, Utah. Las Vegas, NV: Univ. of Nevada. Unpublished thesis. Lists 1207 taxa for 621,762 ha; annotations of plant list include habitat, local distribution, floristic component, synonymy, community type, collector, and collection date and number. Reviews history of botanical collection. Discusses physiography and geology; divides county into six topographic units and discusses the elevational range, accessibility, geology, and watersheds of each. Describes climate and soils and discusses climatic and edaphic factors affecting plant distribution. Describes community types and plant associations; discusses impact of grazing and land use on vegetation. Defines floristic components.

Meyer, S. E. 1980. Capitol Reef National Park, revised working checklist. Torrey, UT: Capitol Reef National Park. Available from Capitol Reef National Park, Torrey, UT. Lists 472 taxa; plant list annotated with common names.

Nebeker, G. T. 1975. Manual of the flora of the East Tintic Mountains, Utah. Provo, UT: Brigham Young Univ. Unpublished thesis. Lists 211 taxa; annotations include habitat, geographic range, collection number. Briefly discusses topography, geology, plant communities. Includes keys to species.

Nelson, R. A. 1976. Plants of Zion National Park. Springdale, UT: Zion Natural History Association. Available from Zion National Park, Springdale, UT. Lists 704 taxa for 59,307 ha; annotations include species descriptions, local distribution, relative abundance, habitat, and common names. Describes vegetation zones, discusses phenology. Includes keys to species, glossary of botanical terms, photographs of plant communities, and line drawings of many plants.

Preece, S. J., Jr. 1950. Floristic and ecological features of the Raft River Mountains of northwestern Utah. Salt Lake City, UT: Univ. of Utah. Unpublished thesis. Lists 341 taxa; annotations include relative abundance, habitat, elevational range, collector, and collection location and number.

Describes topography and geology. Discusses history of botanical collection; vegetation types, correlating vegetation with substrate, climate, and grazing; and floristic elements and relation of flora to paleoclimate. Includes photographs of vegetation.

WELSH, S. L. 1957. An ecological survey of the vegetation of the Dinosaur National Monument, Utah. Provo, UT: Brigham Young Univ. Unpublished thesis. Lists 360 taxa for 30,352 ha; annotations of plant list include geologic formation, habitat, associated species, elevation, collector, and collection location and number. Describes geology, topography, and climate. Describes plant communities on different geological formations. Lists major species of each plant community, discusses trends in succession and edaphic factors in plant distribution. Includes photographs of geomorphological features, vegetation map, topographic map, and geological map.

WELSH, S. L., AND G. MOORE. 1968. Plants of Natural Bridges National Monument. Proc. Utah Acad. Sci., Arts, and Letters 45:220–248. Lists 224 taxa for 3148 ha; annotations of plant list include common names, relative abundance, habitat, collector, and collection location, date, and number. Describes plant communities in relation to topography and habitat.

LITERATURE CITED

BOWERS, J. E. 1981. Local floras of Arizona: an annotated bibliography. Madroño. 28:193–209.

CHRISTENSEN, E. M. 1967a. Bibliography of Utah botany and wildland conservation. Brigham Young Univ. Sci. Bull., Biol. Ser. 9(1):1–136.

———. 1967b. Bibliography of Utah botany and wildland conservation, No. II. Proc. Utah Acad. Sci., Arts, and Lett. 44:545–566.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, J. L. REVEAL, AND P. HOLMGREN. 1972. Intermountain flora: vascular plants of the Intermountain Region, USA. Vol. 1. Hafner, New York.

———. 1977. Intermountain flora. Vol. 6. Columbia Univ. Press, New York.

EWAN, J. 1936. Bibliography of the botany of Arizona. American Midland Naturalist 17:430–454.

HARRINGTON, H. D. 1954. Manual of the plants of Colorado. 2d ed. Sage Books, Denver, Colorado.

HOFFMAN, G. R., AND G. J. TOMLINSON. 1966. A bibliography of vegetational studies of Colorado. Southwestern Naturalist 11:223–237.

HOLMGREN, A. H., AND J. L. REVEAL. 1966. Checklist of the vascular plants of the Intermountain Region. U.S. Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah. Research Paper No. 32.

JAEGER, E. C. 1941. Desert wild flowers. Rev. ed. Stanford Univ. Press, Stanford, California.

KEARNEY, T. H., AND R. H. PEEBLES. 1942. Flowering plants and ferns of Arizona. U.S. Dept. of Agriculture, Washington, D.C. Miscellaneous Publication No. 423.

———. 1960. Arizona flora. Univ. of California Press, Berkeley, California.

MARTIN, W. C., AND C. R. HUTCHINS. 1981. Flora of New Mexico. Lubrecht and Cramer, Monticello, New York.

SCHMUTZ, E. M. 1978. Classified bibliography on native plants of Arizona. Univ. of Arizona Press, Tucson, Arizona.

SHREVE, F., AND I. L. WIGGINS. 1964. Vegetation and flora of the Sonoran Desert. Stanford Univ. Press, Stanford, California.

TIDESTROM, I. 1925. Flora of Utah and Nevada. U.S. Nat. Herb. Contrib. 25.

TIDESTROM, I., AND T. KITTELL. 1941. A flora of Arizona and New Mexico. Catholic Univ. of America Press, Washington, D.C.

U.S. FISH AND WILDLIFE SERVICE. 1977a. Annotated bibliography of natural resources information: northwestern New Mexico. FWS/OBS-77/33.

———. 1977b. Annotated bibliography of natural resources information: southern Utah. FWS/OBS-77/34.

———. 1977c. Annotated bibliography of natural resources information: northwestern Colorado. FWS/OBS-77/35.

WELSH, S. L., AND G. MOORE. 1973. Utah plants; tracheophyta. Brigham Young Univ. Press, Provo, Utah.

ACKNOWLEDGMENTS

I thank Dr. Donald Pinkava, Dr. Stanley Welsh, Dr. William Martin, and Dr. Arthur Holmgren for reviewing the manuscript and suggesting additional floras. I also thank Dr. Elizabeth Neese, Dr. Lois Arnow, Dr. Kimball Harper, and Dr. Beverly Albee, who provided several floras. The interlibrary loan personnel at the University of Arizona Library obtained many books and theses for me, and without their invaluable assistance I could not have compiled this bibliography.

THE RELATION BETWEEN SPECIES NUMBERS AND ISLAND CHARACTERISTICS FOR HABITAT ISLANDS IN A VOLCANIC LANDSCAPE

Steven H. Carter-Lovejoy[1]

ABSTRACT.— Within the Craters of the Moon Lava Flow in southeastern Idaho are kipukas, islands of sagebrush habitat isolated by relatively barren lava. In 1979 I counted the number of species of plants, small mammals, and reptiles for a series of kipukas. The degree of isolation of a kipuka was not related to numbers of species found there; thus, these data do not support the equilibrium theory of island biogeography. For most of the study organisms lava is not a significant barrier to dispersal. Larger kipukas support larger numbers of species. For plants this relationship likely is a result of the increased topographic variety of larger kipukas, whereas for small mammal species minimum area requirements for maintaining populations are met only by larger kipukas. More distant kipukas showed increased density of small mammals, possibly as a result of reduced predation. Patterns of distribution in this ecosystem are best explained, not by any all-inclusive community mechanism, but through the agglomerative contributions of a variety of population and community functions.

The Snake River Plain in Idaho is a formation built up, over millions of years, of windblown loess deposits alternating with layers of volcanic materials from localized eruptions (Greeley and King 1975). The present manifestation of this geologic history is a complex and heterogeneous combination of soils and surfaces, ranging from well-drained loess soils dozens of feet deep to bare lava rock surfaces. The distribution of vegetation is dictated by this physiographic heterogeneity; species found growing on a lava surface differ from those found in a deep crevice in the lava surface, and both sets of species differ from species found on deep soil that might occur a few meters away. The distribution of animals also reflects the heterogeneity of their environment, both physical and floral. The impact of edaphic complexity on plant and animal distributions is enhanced by unevenly distributed sources of dispersal.

Kipuka is a name given to an area of older land surrounded by but not buried by more recent lava flows. Within the most recent lava flows on the Snake River Plain, kipukas present striking contrasts in landscapes. The approximately 150,000 ha lava surface of the Craters of the Moon Flow is about 2000–2500 years old (Prinz 1970)—recent enough, in the cold, arid climate of southeastern Idaho, that little soil has accumulated and little vegetative colonization of the lava has taken place (Eggler 1941). Superimposed on this barren landscape are hundreds of kipukas; although these kipukas are diverse in age, edaphic and topographic characteristics, and isolation, all are well vegetated.

In the summer of 1979, I studied the distribution of plants, small mammals, and reptiles on a number of kipukas within the Craters of the Moon Flow in southeastern Idaho. This paper presents data relevant to the question, To what extent does the islandlike nature of kipukas shape the observed floral and faunal distributions?

METHODS

Study sites were located on 14 kipukas situated near the eastern edge of the Craters of the Moon Flow, 4–21 km south of Arco, Idaho (Fig. 1). The area is characterized by a continental climate, with cold winters and hot summers; mean annual precipitation, falling mostly as snow, is only about 25 cm, but it fluctuates considerably from year to year (Lovejoy 1980). The region lies within Kuchler's (1975) sagebrush-steppe vegetation zone;

---

[1] Department of Biology, Idaho State University, Pocatello, Idaho 83209. Current address: Department of Biological Science, Florida State University, Tallahassee, Florida 32306.

dominant shrubs are *Artemisia tridentata* (big sagebrush) and *A. tripartita* (threetip sagebrush), and dominant grasses are *Agropyron spicatum* (bluebunch wheatgrass) and *Stipa* spp. (needle-and-thread), but the importance of these and of other plant species varies broadly from kipuka to kipuka and even within kipukas.

The study kipukas range in size from 0.16 to 3.6 ha and are separated from the nearest off-lava vegetation by 70–1800 m. From one to four study plots were established on each kipuka. An effort was made to represent adequately the subjectively perceived environmental diversity on each kipuka. Slope and aspect of each plot were measured and soil character measures made.

Vegetation was sampled by canopy-cover estimation (Daubenmire 1959, Hanley 1976). Percent cover of all perennial plants was estimated for 30 0.2 by 0.5 m quadrats situated systematically within each study plot. Species recorded during the systematic samplings were added to the comprehensive species list developed by a walking survey for each kipuka. The total plant species pool of the study area is small; fewer than 80 species on lava or kipukas were encountered during the field study, so the species lists are rather complete.

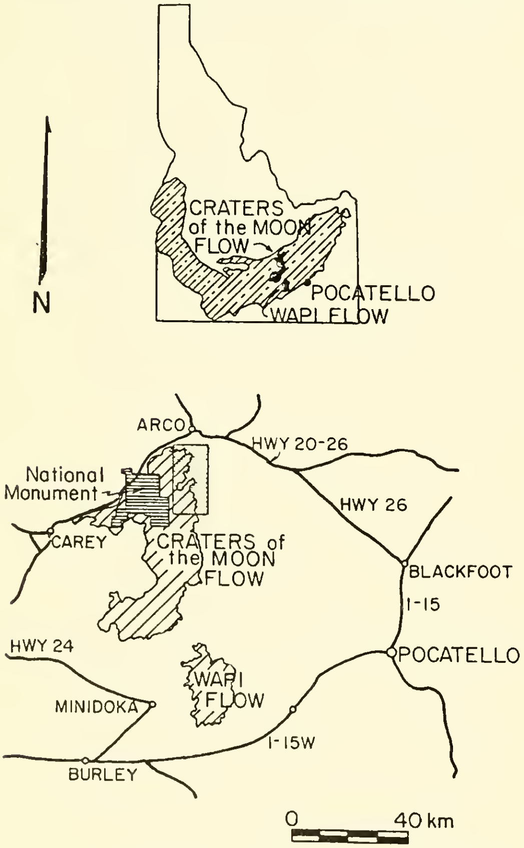


Fig. 1. a, The Snake River Plain in southern Idaho, shown with hatchmarks. b, Recent lava flows in southeastern Idaho. The study kipukas are located within the stippled area.

In each plot, 18 trapping stations were located 10 m apart in a 6 by 3 grid, and three Museum Special snap traps and one McGill rat trap were set at each station. Bait was peanut butter and rolled oats; after a three-day prebait period, traps were checked and reset for three or four nights. Additional traps were located in likely areas on some kipukas and in some lava areas between kipukas and the mainland. Trapping was done within a six-week period (May–June) to minimize the potential for seasonal differences in captures among kipukas (Smith et al. 1975, Johnson 1977). Lizard populations were assessed on six kipukas with unbaited pitfall traps. Lizards captured were marked and released, but marked lizards were never recaptured. Species lists of reptiles and of small mammals were augmented by personal sightings.

Results

The number of plant species on the kipukas ranged from 25 to 49. The number of plants on a kipuka is significantly related to the size of the kipuka (Fig. 2), but not to the degree of isolation of the kipuka (Table 1). The prominent vegetative patterns were related to edaphic and topographic characteristics; these patterns were present within as well as among kipukas (Lovejoy 1980). A companion paper presents the results of ordinations used to explore these patterns (Carter-Lovejoy, in preparation).

Reliable assessments were made of the presence of eight species of small mammals and two lizard species on appropriately trapped kipukas. The number of lizard species on the six pitfall-trapped kipukas ranged from zero to two; species captured were *Sceloporus graciosus* (sagebrush lizard) and *Eumeces skiltonianus* (western skink). The number of small mammals on a kipuka ranged from three to seven. Four species were widely distributed. *Peromyscus maniculatus* (white-footed deer mouse) was captured wherever traps were set, and *Eutamias minimus* (least chipmunk) was caught in most localities. As a result of their larger sizes, *Neotoma cinerea* (bushy-tailed woodrat) and *Sylvilagus nuttalli* (Nuttall's cottontail) were captured less often; however, S. *nuttalli* individuals were observed on every kipuka, and characteristic urine markings of *N. cinerea* were also ubiquitous. Four other species were captured less often: *Perognathus parvus* (Great Basin pocket mouse) was captured on two kipukas, *Microtus montanus* (montane vole) on four, *Reithrodontomys megalotis* (western harvest mouse) on one, and *Spermophilus townsendii* (Townsend's ground squirrel) was caught on three kipukas and sighted on a fourth.

As with the plant species number, the number of small mammal species on a kipuka is positively correlated with size of the kipuka (Fig. 3). The number of mammal species on a kipuka is not correlated with isolation of the kipuka, however (Table 1).

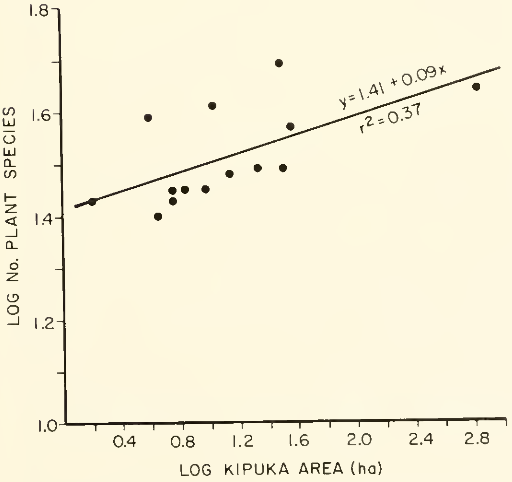


Fig. 2. Species-area effect: number of plant species on a kipuka as a function of the size of the kipuka. $P < 0.05$.

DISCUSSION

The equilibrium theory of island biogeography (MacArthur and Wilson 1967) postulates that the number of species on an island is determined by a dynamic equilibrium between immigration rate and extinction rate. The theory further maintains that two physical measures, island isolation and island size, successfully predict species immigration and extinction rates. Since its conception this theory has been widely accepted and applied by ecologists; it has recently been seriously challenged, however, for its feeble empirical support (Gilbert 1980). The equilibrium theory has been applied to several types of habitat island, often with inconsistent and poorly interpreted results (see Gilbert 1980). In this study the theory-derived prediction that more isolated kipukas have fewer species is not borne out.

Application of the MacArthur-Wilson species-isolation model has rarely been made to plants (Simberloff 1974, but see Crowe 1979). The persistence of individuals of perennial species is long relative to immigration rates. Only in systems with very broad barriers to plant dispersal or with short-lived plants dominant would the presumed isolation effect be important. Certainly Snake River Plain vegetation and the system of lava

TABLE 1. Small mammal and plant species numbers for kipukas that are grouped into size classes and arranged according to degree of isolation.

Kipuka name	Size (ha)	Distance to M.L.[a] (m)	No. mammal species[b]	No. plant species
2	.45	70	3	25
7	.16	350[d]	5	27
4	.40	400	3	39
13	.69	550	4	28
14	.57	560	4	31
9	.57	1490	4	27
1	1.4	160	5	30
5	1.1	410	4	41
15[c]	2.2	670	4	31
10	.97	1800	5	28
6	3.1	220	7	49
8	3.6	500	6	37
15[c]	2.2	670	4	31
16	3.2	1270	6	31

[a] Distance to mainland: shortest direct-line distance across lava.

[b] Number of small mammal species: numbers include *Neotoma cinerea* and *Sylvilagus nuttalli*, presumed present on every kipuka.

[c] Kipuka 15 is placed in two size classes because of its intermediate size.

[d] Only 70 m from kipuka 6.

barriers do not fit these models. Immigration of plant propagules into kipukas probably differs little from the cross-seeding that occurs among the heterogeneous habitats of the Snake River Plain.

If an isolation effect did occur, one would be more likely to observe it with small mammals; I did not observe an isolation effect. It is worthwhile to evaluate to what degree lava acts as a barrier to small mammal dispersal. *Eutamias minimus*, *P. maniculatus*, *S. nuttalli*, and *N. cinerea* were captured in traps set on lava. Scat and urine markings of the latter two species were frequently sighted up to several kilometers from any kipuka or mainland, and it is quite possible that the latter three nest and breed on lava; certainly *N. cinerea* does. Although the small amount of vegetation on the lava may limit population sizes of these four species on lava, it apparently does not restrict their ability to disperse across it.

If kipukas are not functional isolates but are, at best, the most favorable patches within a matrix of suitable habitat, then extinction on a kipuka is unlikely; indeed, in this context "extinction" has little meaning. Since individuals of these four readily dispersing species made up over 96 percent of all small mammal captures, examination of aggregate small mammal data should obviously reveal no isolation effect.

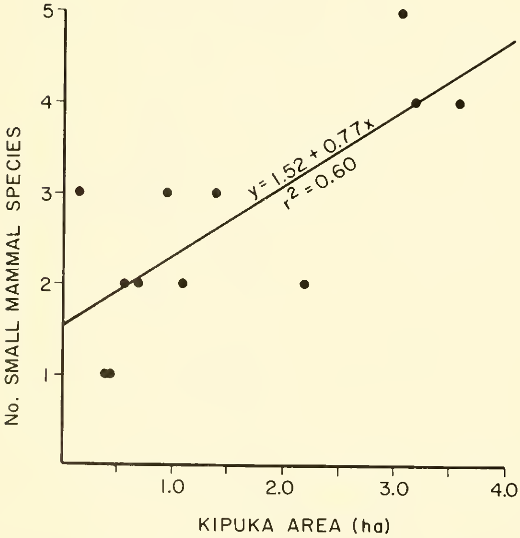


Fig. 3. Species-area effect: number of small mammal species on a kipuka as a function of the size of the kipuka. $P < 0.01$.

It is much less likely that the four other small mammal species trapped here actually reside on lava. One *M. montanus* individual was sighted one night on lava less than 50 m from both a kipuka and the mainland; in no other instance were any of these species sighted or captured on lava. On the other hand, they were not very commonly sighted on kipukas either. Only 24 individuals of these four species were captured. Given the high trapping intensity on kipukas, it is possible to assume that individuals representing the sole capture of their species on any kipuka are immigrants to the kipuka, not members of established populations. There were 11 encounters of these four species during the study; in only 4 cases were we sampling a population (conservatively defined as two or more individuals). The other 7 encounters were of single individuals, despite exhaustive trapping of the habitats in which these individuals were found.

Isolation seemed to play no role in the presence of the two lizard species found on the kipukas either. On the other hand, on no kipuka did we find the diurnal and conspicuous *Phrynosoma douglassi* (desert short-horned lizard), even though it was frequently sighted on mainland; its total absence on kipukas suggests that lava is more of a barrier to the dispersal of this slow-moving lizard than it is to the dispersal of the two quicker species.

One interesting and unexpected isolation effect does exist: the density of animals is significantly and positively correlated with isolation (Fig. 4). Common explanations for so-called "density compensation" (MacArthur 1972) are not appropriate in light of the fact that the density measure, individuals per 100 trap nights, reflects changes in the density of the common species, to which lava is not a barrier. One possible mechanism for increased density on isolated kipukas is reduced predation. Densities of prey for common predators in the area are higher on kipukas than they are on nearby lava, because of the relative abundance of vegetation on kipukas. As a result of this concentration of prey, predators are likely to focus their attention on kipukas. Predation pressure is intermittent, however, particularly on smaller kipukas. Small kipukas (less than 3 ha) are probably not large enough to support a snake population (Lovejoy 1980). We rarely observed birds of prey over the study area, perhaps because of the lack of roosts. Although scat finds indicated that coyotes were occasional visitors to all study kipukas, none of the kipukas is large enough to support a resident coyote. So, between times of possibly intense predation, kipukas may enjoy periods of total release from predation pressure. During these lulls, small mammal populations may be able to build up to densities that greatly exceed densities on less isolated kipukas, where predators may forage more frequently. Certainly this density-isolation phenomenon deserves further study.

Connor and McCoy (1979) discuss three mechanisms that can explain an observed species-area effect. The "habitat-diversity" hypothesis (Williams 1964) postulates that, as increasingly larger areas are sampled, new habitats with associated new species are encountered. According to the "area-per se" hypothesis (Preston 1960, MacArthur and Wilson 1967), population sizes are proportionately smaller on smaller isolates, implying increased probability of species extinctions. An alternative "passive sampling" hypothesis (Connor and McCoy 1979) holds that species number is controlled by passive sampling from a species pool, so that larger areas intercept larger samples than smaller areas. Connor and McCoy consider this a good "null" hypothesis.

The area-per se hypothesis is associated with the equilibrium island biogeography model; the implication is that an ecologically significant rate of species extinction results in a turnover of species. A number of studies (Gilbert 1980:214, cites 23) purport to support the equilibrium model by demonstrating species-area relationships among island groupings, despite the fact that an observation of a species-area relationship made in a temporally limited study cannot demonstrate species turnover and thus cannot distinguish between the three causal hypotheses above. Specific manipulative experimentation is necessary to distinguish among these hypotheses; unfortunately, such experimentation is virtually nonexistent. Without such experimentation, one can only speculate about causes for the observed relationship.

Data from this study could be used to support all three hypotheses, without refuting any of them. Certainly environmental heterogeneity increases with increasing kipuka size, because larger kipukas have more topographic variation. Support for the null hypothesis can be noted by looking strictly at the numbers of small mammal immigrants on kipukas of different sizes (Fig. 5). These immigrants have presumably reached the kipukas on which they were found by chance; nevertheless, they show a species-area effect, indicating the kipukas are passively sampling small mammal dispersers.

The area-per se hypothesis also appears to have some application to these data. Perhaps the most intrinsically acceptable explanation for the species-area relationship lies with the population ecology of the different species contributing to species number. Equilibrium theory's contention that extinction rates decline with increasing area is by no means certain; on the other hand, decreasing area will at some point result in the extinction of any

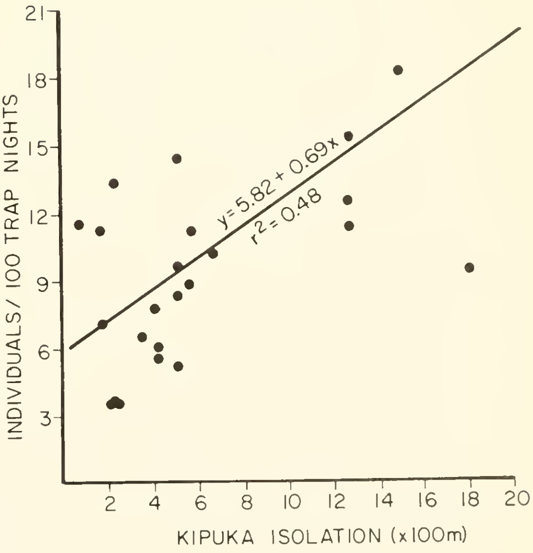


Fig. 4. Density-isolation effect: small mammal density (number of individuals captured for every 100 nights of trapping) as a function of kipuka isolation (straight-line distance to nearest mainland). $P < 0.05$.

particular population. Thus, there must exist some threshold size for each species, below which the probability of extinction of a population of this species is one (Shaffer 1981). Of the small mammal species observed on kipukas for which lava poses an impediment to dispersal, three species appear to have had established populations on at least one kipuka: *P. parvus*, *S. townsendii*, and *M. montanus*. None of these populations was on a kipuka less than three ha in size (Fig. 5). The species involved did not appear to be restricted to a particular type of habitat that was unavailable on smaller kipukas, nor did the increase in environmental heterogeneity on kipukas of larger size appear to be important to the individual species. Instead, it is possible that these species need an area of at least three hectares in this ecosystem to support a large enough number of individuals to maintain a population. Perhaps those species that did not have populations on any of the study kipukas have minimum area requirements larger than three ha.

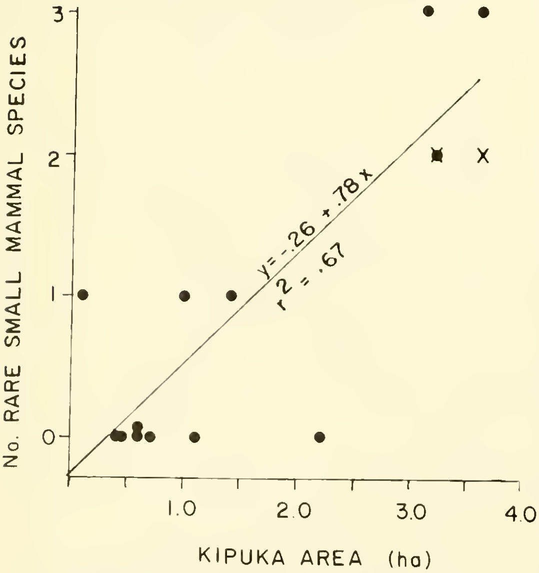


Fig. 5. Species-area effect: number of rare small mammal species on a kipuka as a function of kipuka size. Dots indicate number of species with one or more individuals; X's indicate number of species with two or more individuals. Species considered rare are *P. parvus*, *S. townsendii*, *M. montanus*, and *R. megalotis*. $P < 0.001$.

The minimum size requirements of many species relate to energetics and the available food resource (McNab 1963, Harestad and Bunnell 1979). Species vary in the amount of food required for living and reproducing: larger animals require more food, as do metabolically more active animals. This might account for the absence of *Lepus californicus* (blacktail jackrabbit) and *Dipodomys ordii* (Ord's kangaroo rat) from all study kipukas, even though both species were common on nearby off-lava sites. Animals at higher positions in community trophic structures require more cumulative biomass to stay alive, and populations of such animals will require larger areas in which individuals can forage for food. The absence of the carnivorous (*Onychomys leucogaster* (grasshopper mouse) might be explained by this reasoning. Snakes—*Coluber constrictor* (racer), *Crotalus viridus* (Great Basin rattlesnake), and *Pituophis melanoleucus* (Great Basin gopher snake)—were sighted only on those kipukas or kipuka archipelagos that are greater than three ha in size.

Social behavior is another factor that plays a role in the determination of minimum area requirements, although social behavior is, of course, largely an evolutionary response to energetic considerations. The home range of an animal is an expression of both the social and energetic factors, so that home range sizes, when known, are a rough indication of relative minimum size requirements for small mammals. Literature values for the home range sizes of two mainland species not found on kipukas (1.3–1.4 ha for *O. leucogaster*, 2.7–4.6 ha for *D. ordii* [French et al. 1975]) are considerably larger than those for kipuka-dwelling *P. parvus* (.05–.4 ha [O'Farrell et al. 1975]).

Of course, alternative explanations exist for the absence of the small mammal species that were not found. There might be a lack of suitable habitat on kipukas for some species; for instance, *D. ordii* is generally associated with sandy soils, and only one trapped kipuka met this criterion. If the missing species was absent as well from the mainland immediately adjacent to the lava flow, there would be no ready source of immigrants to colonize kipukas. Lava is probably a very effective, perhaps impenetrable barrier to some species. Certainly the observed distribution of small mammal species can be explained, not through any grand mechanism, but through the agglomerative contributions of a variety of population and community functions. The best understanding of patterns of distribution in the kipuka-lava ecosystem will primarily be elaborated, in the future, by autecological research.

ACKNOWLEDGMENTS

I thank Janice Carter-Lovejoy for her help in the field, Barry Keller for traps and advice, and Dan Simberloff for comments on this paper. I am grateful for the guidance of Dr. Jay E. Anderson throughout this project. This work was completed as part of a contract from the Bureau of Land Management to Idaho State University.

LITERATURE CITED

CONNOR, E. F., AND E. D. MCCOY. 1979. The statistics and biology of the species-area relationship. Amer. Nat. 113:791–833.

CROWE, T. M. 1979. Lots of weeds: insular phytogeography of vacant urban lots. J. Biogeography 6:169–182.

DAUBENMIRE, R. F. 1959. Canopy coverage method of vegetation analysis. Northwest Sci. 33:43–64.

EGGLER, W. A. 1941. Primary succession on volcanic deposits in southern Idaho. Ecol. Monogr. 11:277–298.

FRENCH, N. R., D. M. STODDART, AND B. BOBEK. 1975. Patterns of demography in small mammal populations. Pages 73–102 *in* F. B. Golley, K. Petrusewicz, and L. Ryszkowski, eds., Small mammals: their productivity and population dynamics. Cambridge Univ. Press, New York.

GILBERT, F. S. 1980. The equilibrium theory of island biogeography: fact or fiction? J. Biogeography 7:209–235.

GREELEY, R., AND J. S. KING. 1975. Geologic field guide to the Quaternary volcanics of the south central Snake River plain, Idaho. Idaho Bureau of Mines and Geology, Moscow.

HANLEY, T. A. 1978. A comparison of the line-interception and quadrat estimation methods of determining shrub canopy coverage. J. Range Manage. 31:60–62.

HARESTAD, A. S., AND F. L. BUNNELL. 1979. Home range and body weight—a reevaluation. Ecology 60:389–402.

JOHNSON, W. C. 1977. Examination of censusing techniques for small mammals in a high desert ecosystem. Unpublished thesis. Idaho State Univ., Pocatello.

KUCHLER, A. W. 1975. Potential natural vegetation of the conterminous United States (map). American Geographical Society, New York.

LOVEJOY, S. H. 1980. Patterns in the distribution of plants and animals on lava flows and kipukas in southeastern Idaho. Unpublished thesis. Idaho State Univ., Pocatello.

MACARTHUR, R. H. 1972. Geographical ecology. Harper and Row, New York.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey.

MCNAB, R. K. 1963. Bioenergetics and the determination of home range size. Amer. Nat. 97:133–140.

O'FARRELL, T. P., R. J. OLSON, R. O. GILBERT, AND J. D. HEDLUND. 1975. A population of Great Basin pocket mice, *Perognathus parvus*, in the shrub-steppe of south central Washington. Ecol. Monogr. 45:1–28.

PRESTON, F. W. 1962. The canonical distribution of commonness and rarity. Ecology 43:185–215, 410–432.

PRINZ, M. 1970. Idaho rift system, Snake River plain, Idaho. Geol. Soc. of Amer. Bull. 81:941–948.

SHAFFER, M. L. 1981. Minimum population sizes for species conservation. Bioscience 31:131–134.

SIMBERLOFF, D. S. 1974. Equilibrium theory of island biogeography and ecology. Ann. Rev. Ecol. Syst. 5:161–182.

SMITH, M. H., R. H. GARDNER, J. B. GENTRY, D. W. KAUFMAN, AND M. H. O'FARRELL. 1975. Density estimations of small mammal populations. Pages 25–54 *in* F. B. Golley, K. Petrusewicz, and L. Ryszkowski, eds., Small mammals: their productivity and population dynamics. Cambridge Univ. Press, New York.

WILLIAMS, C. B. 1964. Patterns in the balance of nature. Academic Press, London.

TAXONOMIC STUDIES OF DWARF MISTLETOES (*ARCEUTHOBIUM* SPP.) PARASITIZING *PINUS STROBIFORMIS*

Robert L. Mathiasen[1]

Abstract.— Analysis of morphological characters of *Arceuthobium apachecum* and *A. blumeri* indicates there are several geographically consistent differences between these taxa, which supports their current classification at the specific level. Shoot height and perianth lobe number exhibited considerable geographic variation, and some morphological characters examined were continuous. Peak flowering and seed dispersal periods for these species differed slightly. Altitudinal, seasonal, and latitudinal variations in flowering and seed dispersal were detected and may be responsible for the differences in phenology between these taxa.

Dwarf mistletoes (*Arceuthobium* spp.) are the most serious disease agents of conifers in the southwestern United States. Many of the North American species of *Arceuthobium* were described by Engelmann in the 1800s (Gray 1850, Watson 1880). Gill (1935) prepared the first comprehensive monograph of the genus, in which he reduced several previously recognized fall-flowering species to host forms of *A. campylopodum* Engelm. Gill designated forms of *A. campylopodum* exclusively on the basis of host relationships because he recognized few morphological differences between these taxa. In Gill's system *A. campylopodum* Engelm. forma *blumeri* (Engelm.) Gill encompasses the dwarf mistletoes that parasitize sugar pine (*Pinus lambertiana* Dougl.) and western white pine (*Pinus monticola* Dougl.) in California and Oregon and those that parasitize southwestern white pine (*Pinus strobiformis* Engelm.) in Arizona and New Mexico. Hawksworth and Wiens (1965, 1970, 1972) described several new species of *Arceuthobium* from Mexico and the Western United States and reported that many of Gill's host forms could be distinguished morphologically and physiologically, including *A. campylopodum* f. *blumeri* and f. *cyanocarpum* (A. Nelson) Gill. They separated f. *blumeri* into three species, *A. californicum* Hawksw. & Wiens, *A. apachecum* Hawksw. & Wiens, and *A. blumeri* A. Nelson, based on morphology, phenology, and geographic distribution. *Arceuthobium apachecum* exclusively parasitizes *Pinus strobiformis* and is distributed from the Santa Rita and Chiricahua Mountains of southern Arizona north to east central Arizona and west central New Mexico, with one population known from northern Coahuila, Mexico (Hawksworth and Wiens 1972, Mathiasen 1979). *Arceuthobium blumeri* parasitizes *Pinus strobiformis* and *Pinus ayacahuite* var. *brachyptera* Shaw (Mexican white pine) and is distributed from the Huachuca Mountains, Arizona south through the Sierra Madre Occidental to southern Durango, Mexico, with one population known from Nuevo León, Mexico (Hawksworth and Wiens 1972, Mathiasen 1979). *Arceuthobium apachecum* and *A. blumeri* are morphologically similar, but can be distinguished by shoot color, shoot height, growth habit, and number of perianth lobes of staminate flowers (Hawksworth and Wiens 1972). Few data, however, were available on the phenology of these species (Hawksworth and Wiens 1972), and because of their morphological similarity their specific status has been questioned (Kuijt 1973). This study was undertaken to provide more information on the morphological and physiological characters of these two taxa.

Materials and Methods

Measurements and observations of morphological characters were made on 21 populations of *A. apachecum* and 18 populations of *A. blumeri* distributed throughout their geographic ranges. Specimens examined were collected by the author in 1975 and 1976 or were previously deposited at the U.S. Forest Service, Forest Pathology Herbarium, Fort Collins, Colorado (FPF) or the University of Arizona Herbarium, Tucson, Arizona (ARIZ). The specimens examined represent essentially all the material that has been collected for these species. Measurements and observations were made for the following morphological characters: staminate and pistillate shoot height, pistillate shoot basal diameter, staminate and pistillate shoot color, and shoot growth habit (all measurements and observations for dominant shoots of nonsystemic infections only); length and width of staminate spikes in summer; staminate flower diameter; perianth lobe number and color; mature fruit length, width, and color; mature seed length, width, and color. The original measurements of shoot height made for these taxa by Hawksworth and Wiens (1972) were available and were included in obtaining mean, maximum, and minimum values for this character.

---

[1] School of Forestry, Northern Arizona University, Flagstaff, Arizona 86011.

Observations of flowering and seed dispersal for both species were made in Arizona and New Mexico in the summer and fall of 1973 through 1976. The species, location, elevation, and date were recorded for each field observation, and flowering and seed dispersal were each rated as not started, started but not near peak, near peak, past peak but not completed, and completed. Phenological data were examined by weekly periods for all observations from 1 July through 2 November to determine the approximate periods of flowering and seed dispersal for both species.

RESULTS

Mean heights of staminate and pistillate shoots of *A. blumeri* were approximately 1.5 cm greater than those of *A. apachecum*, and maximum shoot heights of *A. blumeri* were also twice those of *A. apachecum* (Table 1). Nevertheless, analysis of shoot heights for these taxa using the method for comparing two sample means described by Cochran and Cox (1957) for samples with unpaired observations and unequal variance indicates that the differences are not significant at the 5 percent level. Analysis of separate populations from east central Arizona to southern Durango, Mexico, indicates that shoots are smallest for the northern populations of both species and largest for the southern populations (Table 2). In addition, shoot heights are approximately the same for these taxa in southern Arizona (Table 2). Shoots of *A. blumeri* vary in color from light green to straw or gray, and those of *A. apachecum* vary from yellow-green to blue or reddish. Both species parasitize *Pinus strobiformis*, but their growth habit is different on this host. Shoots of *A. apachecum* are consistently densely clustered around the host branch and may even completely obscure the branch. Shoots of *A. blumeri* are more scattered and are rarely densely clustered on a branch.

Lateral staminate spikes are larger for *A. blumeri* (means 12 × 2 mm) than for *A. apachecum* (means 7 × 1 mm). The mean diameter of staminate flowers of *A. blumeri* is larger than that of *A. apachecum*, but their

TABLE 1. Comparison of selected morphological characters of *Arceuthobium apachecum* and *Arceuthobium blumeri*.

	A. apachecum					*A. blumeri*				
CHARACTER	Mean	Max.	Min.	No. populations sampled	No. measured	Mean	Max.	Min.	No. populations sampled	No. measured
Shoot height (cm)										
Pistillate	4.7	9.5	2.5	21	254	6.1	18.0	3.0	18	218
Staminate	3.4	7.5	2.0	16	194	5.0	16.0	2.0	14	107
Shoot basal diameter (mm) (Pistillate)	1.7	4.4	0.8	21	234	2.0	3.4	1.2	18	193
Staminate flower diameter (mm)	2.9	4.2	2.2	10	296	3.2	4.4	2.0	6	146
Mature fruit (mm)										
Length	3.2	4.0	2.6	14	310	3.5	4.0	2.0	10	175
Width	1.9	2.4	1.4	14	310	2.0	2.4	1.6	10	175

size range is approximately the same (Table 1). Perianth lobe dimensions are similar also, but their color varies. In *A. apachecum* the perianth lobes are the same color as the male shoots, but in *A. blumeri* they are darker. These species also differ in the number of perianth lobes. *Arceuthobium apachecum* is predominantly 3-merous (65 percent), commonly 4-merous (33 percent), and rarely 5-merous (2 percent); *A. blumeri* is predominantly 4-merous (53 percent), less commonly 3 or 5-merous (31 percent and 15 percent, respectively), and rarely 6-merous (1 percent). Comparison of perianth lobe number in separate populations from east central Arizona to southern Durango, Mexico, indicates that 3-merous staminate flowers predominate in the northern populations of *A. apachecum* and gradually change until 4-merous flowers predominate in most of the southern populations of this species (Table 3). Four-merous flowers predominate in the most northern populations of *A. blumeri*, but the few counts made for this species in Mexico indicate that 3-merous flowers may predominate in the southern populations. Six-merous flowers were found only in the Arizona population of *A. blumeri* (Huachuca Mountains).

Fruits are approximately the same size for both species (Table 1). Mean dimensions of mature seed were similar also (2.6 × 1.1 mm for *A. blumeri* and 2.3 × 1.0 mm for *A. apachecum*), but seeds of *A. blumeri* are dark green and those of *A. apachecum* are light green. Seeds from Mexican populations of *A. blumeri* were not available for examination, however.

TABLE 2. Geographic variation in shoot height of *Arceuthobium apachecum* and *Arceuthobium blumeri*.

LOCATION (Latitude)	Pistillate (cm)		Staminate (cm)		No. populations sampled
	Mean	Max.	Mean	Max.	
	A. apachecum				
White Mountains, Arizona Mogollon Mountains, New Mexico (33°20′–34°10′N)	4.0	5.0	3.1	4.3	6
Mangas Mountains, New Mexico (34°5′N)	4.1	5.0	2.0	3.0	2
Magdalena and San Mateo Mountains, New Mexico (34°N)	4.7	6.0	3.7	4.5	2
Capitan Mountains, New Mexico (33°30′N)	4.2	5.5	2.0	4.0	2
Pinaleno Mountains, Arizona (32°30′N)	4.2	5.0	3.7	4.4	2
Santa Catalina Mountains, Arizona (32°25′N)	5.8	7.5	4.3	6.1	2
Chiricahua Mountains, Arizona (31°50′N)	4.9	6.0	4.2	5.0	2
Santa Rita Mountains, Arizona (31°40′N)	6.3	9.5	4.9	7.5	3
	A. blumeri				
Huachuca Mountains, Arizona (31°30′N)	6.4	8.5	4.2	8.0	3
Sierra de Ajos, Sonora, Mexico (30°30′N)	6.0	7.5	–	–	1
Chihuahua, Mexico (26°30′–29°30′N)	5.9	11.5	4.7	8.0	8
Durango, Mexico (23°–26°N)	8.0	18.0	7.6	16.0	5

Arceuthobium blumeri consistently flowers earlier than *A. apachecum* (Fig. 1), but one of the most southern populations of *A. apachecum* (Santa Rita Mountains, Arizona) flowers at approximately the same time as the most northern population of *A. blumeri* (Huachuca Mountains, Arizona). These populations are separated by almost 40 miles. *Arceuthobium apachecum* disperses seed somewhat earlier than *A. blumeri* (Fig. 1). Data on the flowering and seed dispersal periods of *A. blumeri* populations in Mexico are still inadequate, but they are evidently similar to the *A. blumeri* population in Arizona (Hawksworth and Wiens 1972). Both species show altitudinal variation in flowering and seed dispersal. Lower populations flower earlier than higher populations in the same mountain ranges in southern Arizona and the reverse is true for seed dispersal. Flowering of *A. apachecum* begins as early as mid-August in the northern populations of this species, but does not start until early September in the southern populations observed. Annual climatic variations also influence the phenology of these species. Seed dispersal starts later in years with a late fall.

Discussion

Arceuthobium apachecum and *A. blumeri* are morphologically similar, but differ in color of staminate and pistillate shoots, growth habit, dimensions of lateral staminate spikes, color of perianth lobes, and seed color. Shoot height and number of perianth lobes appear to be discontinuous characters also, but analysis of different populations indicates that considerable geographic variation occurs in these characters. Although mean shoot heights are different for these species, shoots are shortest in the northern populations of *A. apachecum*, tallest in the southern populations of *A. blumeri*, and approximately the same near the geographic boundary between these taxa in southern Arizona. Variation in the number of perianth lobes appears to follow a geographic pattern also, but more information is needed for Mexican populations of *A. blumeri*. Six-merous flowers are only known for *A. blumeri*, however.

Periods of flowering and seed dispersal for *A. apachecum* and *A. blumeri* are slightly different, although one population of *A. apachecum* does flower at approximately the same

Table 3. Geographic variation in number of perianth lobes of *Arceuthobium apachecum* and *Arceuthobium blumeri*.

Location (Latitude)	3	4	5	6	No. populations sampled	No. measured
	A. apachecum (%)					
White Mountains, Arizona (33°20′–34°10′N)	81	19	0	0	6	390
Pinaleno Mountains, Arizona (32°30′N)	68	30	2	0	2	50
Chiricahua Mountains, Arizona (31°50′N)	42	54	4	0	2	50
Santa Catalina Mountains, Arizona (32°25′N)	54	42	4	0	2	480
Santa Rita Mountains, Arizona (31°40′N)	43	48	8	0	3	500
	A. blumeri (%)					
Huachuca Mountains, Arizona (31°30′N)	30	53	16	1	3	700
Chihuahua, Mexico (26°30′–29°30′N)	40	58	2	0	5	50
Durango, Mexico (23°–26°N)	55	44	1	0	5	100

time as *A. blumeri* in Arizona. Latitudinal variation, however, may influence these differences in flowering and seed dispersal. *Arceuthobium blumeri* has a more southerly range and flowers before *A. apachecum*, but disperses seed slightly later. This pattern is evident in the elevational variation observed for both taxa where lower populations begin flowering before higher populations in the same mountain ranges, but disperse seed sooner at the higher elevations. Scharpf (1965) reported a similar altitudinal relationship for flowering and seed dispersal of *A. abietinum* Engelm. ex Munz in California. Northern populations of *A. apachecum* start seed dispersal before southern populations of this species in Arizona, which also suggests that latitude influences this character. Therefore, the slight differences in the flowering and seed dispersal periods of these species, and possibly other fall-flowering species in the Series *Campylopoda* Hawksw. & Wiens (Hawksworth and Wiens 1970, 1972) may be a result of climatic fluctuations, possibly temperature variation (Scharpf 1965), associated with latitudinal, altitudinal, or seasonal differences. Variation in the flowering and seed dispersal periods of dwarf mistletoes is complex and deserves more study before phenology can play an important role in the classification of fall-flowering species of *Arceuthobium*.

Environmental factors may influence other physiological characters of dwarf mistletoes. The consistent inducement of witches' brooms by *A. apachecum* and the rare inducement of brooms by *A. blumeri* was considered as a taxonomically significant discontinuity between these species by Hawksworth and Wiens (1972). Some populations of both species rarely cause brooms at lower elevations, however, but frequently cause brooms at higher elevations (Mathiasen 1979). The reason for this apparent relationship between witches' broom formation and elevation is unknown, but the rare inducement of brooms by *A. blumeri* reported by Hawksworth and Wiens is not typical of that species.

Geographic variation in morphological and physiological characters of dwarf mistletoes may be influenced by variation in their host population as well as parasitism of different hosts. Shoot height of dwarf mistletoes is directly related to variation in host vigor (Hawksworth 1960, Hawksworth and Wiens

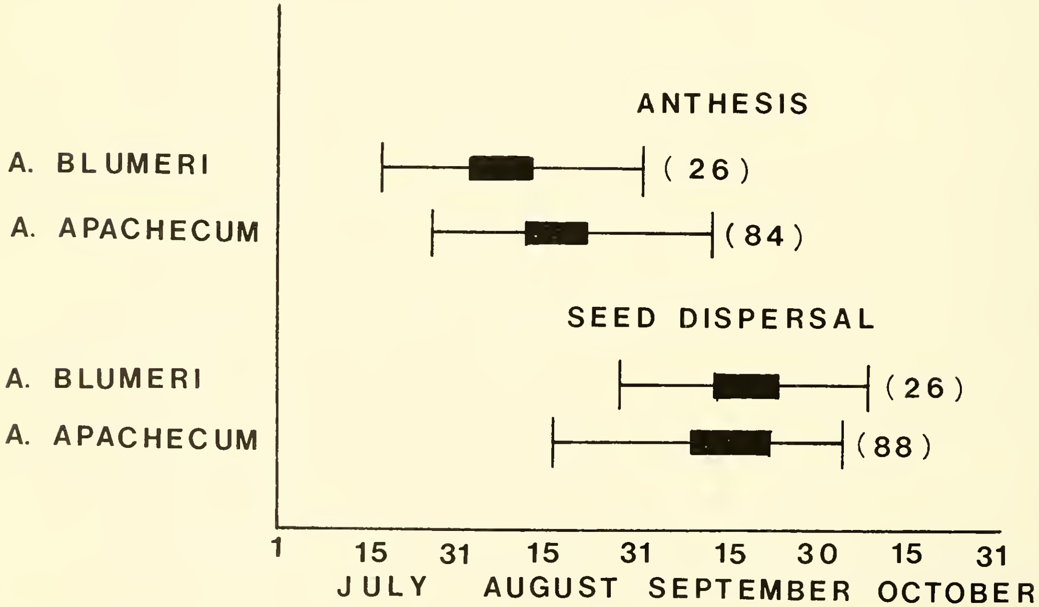


Fig. 1. Approximate periods of anthesis and seed dispersal of *Arceuthobium blumeri* and *Arceuthobium apachecum*. Peak periods are shown by solid bars. Number of observations are in parentheses.

1972) and may itself influence other characters of a dwarf mistletoe. The southern populations of *A. blumeri* parasitize *Pinus ayacahuite*, which is one of the largest pines in Mexico (Loock 1950, Mathiasen 1979). *Pinus ayacahuite* commonly occurs in moist localities, with deep, well-drained soils that are conducive to maintaining a vigorous growth rate (Loock 1950). Therefore, the large shoot heights found in the southern populations of *A. blumeri* may be related to the parasitism of a more vigorous host population. The taxonomic relationships between *P. ayacahuite* and *P. strobiformis* are uncertain. Morphological and physiological variation has been reported in different populations of *P. strobiformis* (Andresen and Steinhoff 1971) and the various taxonomic treatments of this species in different parts of its range suggest that it is quite variable (Steinhoff and Andresen 1971). Critchfield and Little (1966) considered all white pine populations from Durango, Mexico, northward to the southwestern United States to be *P. strobiformis*. Nevertheless, other investigators believe that many of the white pine populations in northern Mexico are typical of *P. ayacahuite* (Martinez 1948, Loock 1950, Mathiasen 1979). Further taxonomic studies of the white pine populations represented in the southwestern United States and northern Mexico are needed and may provide additional information concerning the relationships between *A. blumeri* and *A. apachecum*.

Hawksworth and Wiens (1972) originally considered that the dwarf mistletoes parasitizing *P. strobiformis* might represent a single variable taxon. They finally concluded that *A. apachecum* and *A. blumeri* warranted separate taxonomic status at the specific level, because they believed the morphological and physiological differences they detected between these taxa were geographically consistent. Hawksworth and Wiens (1972) considered two criteria as the most important factors in delimiting species of *Arceuthobium*: (1) species maintain their morphological integrity when parasitizing species other than their principal hosts, and (2) species of *Arceuthobium* are often sympatric but do not show evidence of hybridization. It is not known if *A. apachecum* and *A. blumeri* meet these criteria because they are not sympatric and do not parasitize any species other than their principal hosts (Hawksworth and Wiens 1972, Mathiasen 1979). Hawksworth and Wiens (1972), however, reported that these taxa maintain their morphological integrity when grown under common greenhouse conditions. In addition, chemical analysis of the shoots of these species has shown there are consistent differences in their phenolic chemistry (Hawksworth and Wiens 1972, Crawford and Hawksworth 1979). Artificial hybridization of *A. apachecum* and *A. blumeri* has been attempted, but the results were inconclusive (Mathiasen, unpubl. ms.). Crosses between *A. apachecum* (staminate) and *A. blumeri* (pistillate) were destroyed by a wildfire in the Huachuca Mountains, Arizona, in 1977 before results could be assessed. Crosses between *A. blumeri* (staminate) and *A. apachecum* (pistillate) in the Santa Catalina Mountains, Arizona, resulted in no successful fruit set, but the control crosses (*A. apachecum* [staminate] × *A. apachecum* [pistillate]) yielded very poor fruit set. These investigations must be repeated before their results can be considered as evidence these species are reproductively incompatible.

Although geographic variation occurs in some of the morphological and physiological characters used by Hawksworth and Wiens to delimit *A. apachecum* and *A. blumeri*, the results of this study indicate there are several geographically consistent morphological discontinuities between these taxa. I believe these morphological differences are taxonomically significant and suggest that these dwarf mistletoes should be given separate taxonomic recognition. Nevertheless, these populations may represent intermediate stages of gradual evolutionary divergence, and perhaps their recognition at the subspecific level would be more representative of their natural relationship.

Hawksworth and Wiens (1972) defined subspecies of *Arceuthobium* as "geographically restricted populations, delimited by relatively few but consistent variations." The dwarf mistletoe populations parasitizing *Pinus strobiformis* appear to more closely conform to these criteria than those used by Hawksworth and Wiens to define species of *Arceuthobium*. Examination of the discontinuities separating currently recognized subspecies of *Arceuthobium* (Hawksworth and Wiens 1970, 1972, 1977) indicates there are more morphological and physiological differences between these taxa than between *A. apachecum* and *A. blumeri.* Several species in the Series *Campylopoda,* however, including *A. apachecum* and *A. blumeri,* are delimited by relatively few morphological and physiological differences, so the classifi cation of taxa in this series is relatively consistent. Because species and subspecies of *Arceuthobium* differ only in the number of discontinuities between them (Hawksworth and Wiens 1972), the elevation of currently recognized subspecies to specific rank or the separation of some species into subspecies would alleviate the apparent inconsistencies I feel exist in the present classification of *Arceuthobium.* Consistency in the classification of a group is desirable and changes in the rank of taxa for motives of consistency or for achieving a more balanced natural classification are justified (Davis and Heywood 1963). Isozyme analyses and additional field studies of dwarf mistletoe populations in Mexico and the western United States are in progress, and the results may provide evidence that changes in the rank of some taxa would create. a more natural and consistent classification of the genus (F. G. Hawksworth and Dan Nikrent, pers. comm., 1981). Therefore, I do not feel that a change in the rank of *A. apachecum* or *A. blumeri* should be considered until additional information is available concerning their natural relationships and their relationship with other species in the Series *Campylopoda.*

Stability in the classification of such an economically important group as *Arceuthobium* is desirable; yet it is doubtful that this can be achieved in the near future because little is known about the ranges and natural relationships of the recently discovered Mexican and Central American species (Hawksworth and Wiens 1972, 1977, 1980). More than one-half of the taxa now recognized have been described in the last 10 to 15 years, so much critical work on the entire genus will be required before a more stable classification of *Arceuthobium* can be achieved.

ACKNOWLEDGMENTS

This research was supported by the U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, and the University of Arizona, Department of Plant Pathology. I would particularly like to thank F. G. Hawksworth for his support and constructive comments regarding the final manuscript. Our discussions concerning the taxonomy of *Arceuthobium* have greatly contributed to this work.

LITERATURE CITED

Andresen, J. M., and R. J. Steinhoff. 1971. The taxonomy of *Pinus flexilis* and *Pinus strobiformis.* Phytologia 22: 57–70.

Cochran, W. G., and G. M. Cox. 1957. Experimental designs, 2d ed., John Wiley & Sons, Inc., New York.

Crawford, D., and F. G. Hawksworth. 1979. Flavonoid chemistry of *Arceuthobium* (Viscaceae). Brittonia 31:212–216.

Critchfield, W. B., and E. L. Little. 1966. Geographic distribution of the pines of the world. U.S. Dept. Agric., Misc. Publ. 991, 97 pp.

Davis, P. H., and V. H. Heywood. 1963. Principles of angiosperm taxonomy. Oliver and Boyd, Princeton, New Jersey.

Gill, L. S. 1935. *Arceuthobium* in the United States. Connecticut Acad. Arts and Sci. Trans. 32: 111–245.

Gray, A. 1850. Plantae Lindheimerianae. Part II. Boston J. Natur. Hist..6: 141–240.

Hawksworth, F. G. 1960. Growth rate of dwarf mistletoe infections in relation to the crown class of the host U.S. Dept. Agric. For. Serv., Res. Note RM-41, 4 p., Rocky Mtn. For. and Range Exp. Stn., Fort Collins, Colorado.

Hawksworth, F. G., and D. Wiens. 1965. *Arceuthobium* in Mexico. Brittonia 17: 213–238.

———. 1970. New taxa and nomenclatural changes in *Arceuthobium* (Viscaceae). Brittonia 22: 265–269.

———. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). U.S. Dept. Agric. For. Serv., Agric. Handb. 401, 234 pp.

———. 1977. *Arceuthobium* (Viscaceae) in Mexico and Guatemala: additions and range extensions. Brittonia 29: 411–418.

———. 1980. A new species of *Arceuthobium* (Viscaceae) from central Mexico. Brittonia 32: 348–352.

Kuijt, J. 1973. Review of "Biology and classification of dwarf mistletoes (*Arceuthobium*)" by F. G. Hawksworth and D. Wiens. 1972. Madrono 22: 34-35.

Loock, E. E. M. 1950. The pines of Mexico and British Honduras. Union South Africa Dept. For. Bull. 35, 244 pp.

Martinez, M. 1948. Los pinos Mexicanos. Ed. 2 Mexico, 361 pp.

MATHIASEN, R. L. 1979. Distribution and effect of dwarf mistletoes parasitizing *Pinus strobiformis* in Arizona, New Mexico, and northern Mexico. Southwestern Natur. 24: 455–461.

SCHARPF, R. F. 1965. Flowering and seed dispersal of dwarf mistletoe (*Arceuthobium campylopodum*) in California. U.S. Dept. Agric. For. Serv., Res. Note PSW-68, 6 p., Pac. Southwest For. and Range Exp. Stn., Berkeley, California.

STEINHOFF, R. J., AND J. W. ANDRESEN. 1971. Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silvae Genetica 20: 159–167.

WATSON, S. 1880. Botany in California. II. Pages 105–107 *in Apetalea, Gymnospermae,* Monocotyledonous, or endogenous plants, Cryptogamous plants. Welsh, Bigelow, and Co., Cambridge, Massachusetts.

NOTICE TO CONTRIBUTORS

Manuscripts intended for publication in the *Great Basin Naturalist* or *Great Basin Naturalist Memoirs* must meet the criteria outlined in paragraph one on the inside front cover. They should be directed to Brigham Young University, Stephen L. Wood, Editor, Great Basin Naturalist, 290 Life Science Museum, Provo, Utah 84602. Three copies of the manuscript are required. They should be typewritten, double spaced throughout on one side of the paper, with margins of at least one inch on all sides. Use a recent issue of either journal as a format, and the *Council of Biology Editors Style Manual, Fourth Edition* (AIBS 1978) in preparing the manuscript. An abstract, about 3 percent as long as the text, but not exceeding 200 words, written in accordance with *Biological Abstracts* guidelines, should precede the introductory paragraph of each article.

All manuscripts receive a critical peer review by specialists in the subject area of the manuscript under consideration. Authors may recommend one or two reviewers for their article.

Accepted manuscripts less than 100 printed pages in length will automatically be assigned to the *Great Basin Naturalist*. Those larger than 100 printed pages will be considered for the *Memoirs* series.

Illustrations and Tables. All illustrations and tables should be made with a view toward having them appear within the limits of the printed page. The original illustrations or glossy photoprints of them should accompany the manuscript. Illustrations should be prepared for reduction by the printer to either single-column (2⅝ inches) or double-column (5½ inches) width, with the length not exceeding 7½ inches.

Costs Borne by Contributor. Contributors to the *Great Basin Naturalist* should be prepared to donate from $10 to $40 per printed page toward publication of their article (in addition to reprint costs). Excessive or complex tables requiring typesetting may be charged to the author at cost. Authors publishing in the *Great Basin Naturalist Memoirs* may be expected to contribute $40 per printed page in addition to the cost of the printed copies they purchase. No reprints are furnished free of charge.

Reprint Schedule for the *Great Basin Naturalist*

100 copies, minimum cost for 2 pages, $26.
Each additional 2 pages, $6.
Each additional 100 copies, $4 for each 2 pages.
Examples: 300 copies of 10 pages = $82; 200 copies of 13 pages = $86.

Great Basin Naturalist Memoirs

No. 1 The birds of Utah. By C. L. Hayward, C. Cottam, A. M. Woodbury, H. H. Frost. $10.
No. 2 Intermountain biogeography: a symposium. By K. T. Harper, J. L. Reveal et al. $15.
No. 3 The endangered species: a symposium. $6.
No. 4 Soil-plant-animal relationships bearing on revegetation and land reclamation in Nevada deserts. $6.
No. 5 Utah Lake monograph. $8.
No. 6 The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. $60.

TABLE OF CONTENTS

Utah flora: Rosaceae. Stanley L. Welsh 1

Seasonal foods of coyotes in southeastern Idaho: a multivariate analysis. James G. MacCracken and Richard M. Hansen 45

Structure of Alpine plant communities near King's Peak, Uinta Mountains, Utah. George M. Briggs and James A. MacMahon 50

Observations on the reproduction and embryology of the Lahontan tui chub, *Gila bicolor*, in Walker Lake, Nevada. James J. Cooper 60

The prevalence of *Echinococcus granulosus* and other taeniid cestodes in sheep dogs of central Utah. Lauritz A. Jensen, Ferron L. Andersen, and Peter M. Schantz 65

Growth of juvenile American lobsters in semiopen and closed culture systems using formulated diets. S. R. Wadley, R. A. Heckmann, R. C. Infanger, and R. W. Mickelsen 67

Diameter-weight relationships for juniper from wet and dry sites. T. Weaver and R. Lund 73

A description of Timpie Springs, Utah, with a preliminary survey of the aquatic macrobiota. Thomas M. Baugh, Michael A. Nelson, and Floyd Simpson 77

Vegetation and soil factors in relation to slope position on foothill knolls in the Uinta Basin of Utah. Miles O. Moretti and Jack D. Brotherson 81

Weather conditions in early summer and their effects on September blue grouse (*Dendragapus obscurus*) harvest. Joy D. Cedarleaf, S. Dick Worthen, and Jack D. Brotherson 91

Description of the female of *Phalacropsylla hamata* (Siphonaptera: Hystrichopsyllidae). R. B. Eads and G. O. Maupin 96

First record of pygmy rabbits (*Brachylagus idahoensis*) in Wyoming. Thomas M. Campbell III, Tim W. Clark, and Craig R. Groves 100

Paspalum distichum L. var. *indutum* Shinners (Poaceae). Kelly Wayne Allred 101

Local floras of the southwest, 1920–1980: an annotated bibliography. Janice E. Bowers 105

The relation between species numbers and island characteristics for habitat islands in a volcanic landscape. Steven H. Carter-Lovejoy 113

Taxonomic studies of dwarf mistletoes (*Arceuthobium* spp.) parasitizing *Pinus strobiformis*. Robert L. Mathiasen 120

THE GREAT BASIN NATURALIST

Volume 42 No. 2
June 30, 1982
Brigham Young University

GREAT BASIN NATURALIST

Editor. Stephen L. Wood, Department of Zoology, 290 Life Science Museum, Brigham Young University, Provo, Utah 84602.

Editorial Board. Kimball T. Harper, Chairman, Botany; James R. Barnes, Zoology; Hal L. Black, Zoology; Stanley L. Welsh, Botany; Clayton M. White, Zoology. All are at Brigham Young University, Provo, Utah 84602.

Ex Officio Editorial Board Members. Bruce N. Smith, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications.

Subject Area Associate Editors.

Dr. Noel H. Holmgren, New York Botanical Garden, Bronx, New York 10458 (Plant Taxonomy).

Dr. James A. MacMahon, Utah State University, Department of Biology, UMC 53, Logan, Utah 84322 (Vertebrate Zoology).

Dr. G. Wayne Minshall, Department of Biology, Idaho State University, Pocatello, Idaho 83201 (Aquatic Biology).

Dr. Ned K. Johnson, Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720 (Ornithology).

Dr. E. Philip Pister, Associate Fishery Biologist, California Department of Fish and Game, 407 West Line Street, Bishop, California 93514 (Fish Biology).

Dr. Wayne N. Mathis, Chairman, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 (Entomology).

Dr. Theodore W. Weaver III, Department of Botany, Montana State University, Bozeman, Montana 59715 (Plant Ecology).

The *Great Basin Naturalist* was founded in 1939 and has been published from one to four times a year since then by Brigham Young University. Previously unpublished manuscripts in English of less than 100 printed pages in length and pertaining to the biological natural history of western North America are accepted. Western North America is considered to be west of the Mississippi River from Alaska to Panama. The *Great Basin Naturalist Memoirs* was established in 1976 for scholarly works in biological natural history longer than can be accommodated in the parent publication. The *Memoirs* appears irregularly and bears no geographical restriction in subject matter. Manuscripts are subject to the approval of the editor.

Subscriptions. The annual subscription to the *Great Basin Naturalist* for private individuals is $16.00; for institutions, $24.00 (outside the United States, $18.00 and $26.00); and for student subscriptions, $10.00. The price of single issues is $6.00 each. All back issues are in print and are available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to Brigham Young University, *Great Basin Naturalist,* 290 Life Science Museum, Provo, Utah 84602. The *Great Basin Naturalist Memoirs* may be purchased from the same office at the rate indicated on the inside of the back cover of either journal.

Scholarly Exchanges. Libraries or other organizations interested in obtaining either journal through a continuing exchange of scholarly publications should contact the Brigham Young University Exchange Librarian, Harold B. Lee Library, Provo, Utah 84602.

Manuscripts. See *Notice to Contributors* on the inside back cover.

7-82 650 60479

ISSN 017-3614

MUS. COMP. ZOOL.
LIBRARY
OCT
HARVARD
UNIVERSITY

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 42 June 30, 1982 No. 2

UTAH PLANT TYPES—HISTORICAL PERSPECTIVE 1840 TO 1981—ANNOTATED LIST, AND BIBLIOGRAPHY

Stanley L. Welsh[1]

ABSTRACT.— Reviewed are the 144 collectors and 167 authors of 1073 Utah vascular plant types for the period from 1840 to 1981. Historical perspective yields evidence of geography of collection activities by botanists who penetrated the boundaries of the state, and of shifting centers of emphasis in the study of Utah plants from a classical taxonomic standpoint. Philosophy and influence of contemporary authors and collectors is discussed as they affect taxonomy of Utah plants in our first 142 years. A short biographical account of Marcus Eugene Jones and his interaction with other American botanists is included. The annotated checklist includes bibliographical citations, type locality data, collector, and place of deposition.

ACKNOWLEDGMENTS

It is impossible to complete a work as complex and tedious as this without the help of others. I thank the curators of the herbaria visited by me for their hospitality and willingness to help in this work. They are as follows: Elizabeth McClintock and John Thomas Howell (CAS); Robert Thorne (RSA); Ronald Hartman (RM); Patricia K. Holmgren and Rupert C. Barneby (NY); George Russell (US); Lois Arnow and Beverly Albee (UT); Mary Barkworth (UTC); Theodore J. Crovello (NDG); and Richard Pohl and Duane Isely (ISC). I am indebted to George Knaphus and Lois Tiffany who made it possible for me to visit the site of Jones Grove, where Marcus E. Jones lived with his family near Grinnell, Iowa. Acknowledged also is the help of Mrs. Ralph Fleener, who resides currently on the former Jones's property, for the checking of records and dates on markers in the cemetery at Grinnell.

Kaye Thorne, my colleague at the herbarium of Brigham Young University, gave encouragement and help at all times. Mark L. Gabel aided me with research on the life of Charles Christopher Parry. To him I am grateful.

To Mr. Charles Walker, archivist for the family of Publius Virgilius and Lavinia (Burton) Jones, I am grateful for the access he provided me to a published family history including accounts of Marcus E. Jones and his wife, Anna Elizabeth Richardson. Also, he provided me original letters written by both of them, and by a nephew of Jones, Arthur J. Jones, who accompanied him on attenuated field trips by wagon. These have given me insight into Jones's family life and have allowed me to present a portion of the life-style of his wife and family during his intensely goal-oriented life. I shall be forever indebted to Mr. Walker and his family for this insight.

---

[1] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Introduction

All taxonomists, and others who work with plant names, have been hampered by lack of a summary treatment of Utah plant types, their collectors, authors, and places of deposition. The specimens serve to typify the names applied to them by the authors who named and described them. The types are the name-bearing specimens and are indispensible in interpretation of taxonomic limits and concepts; they are necessary for nomenclatural considerations.

There are several kinds of types, but only holotypes and their duplicates, the isotypes, have been included uniformly in the following treatment. I have not tried to distinguish holotypes from isotypes in the designations of place of deposition; that is a taxonomic consideration which is left to the monographer. In many instances the name bearing specimens were not designated as types by the authors and I have followed tradition in citing the original materials as types. Many of the older names have been subjected to lectotypification. Where this has been obvious, mainly in taxonomic revisions or as indicated on some herbarium annotations, I have followed that usage. Lectotypification, however, is subject to interpretation, and the specimens cited might ultimately be excluded from consideration as lectotype or isolectotype. Too, some materials have been cited as cotypes or syntypes. When a portion of the original collection cited is from Utah, I have included that material as a type. It might have been designated at a lower level, i.e., as paratype, by some author or authors unknown to me.

Designation of types is a function of rules established mainly in the 20th-century, and early authors were not impressed with the necessity of typification. Mention of specimens to vouch for newly described taxa was often only incidental. Most of the types serving as bases for taxa described in the 19th-century are now interpreted through lectotypification. Purists often are involved in polemical struggles over selection of the correct portion of the specimens cited (or not cited) as the lectotype. I have not searched all the literature in which lectotypes have been designated; that is the role of the monographer.

I have tried to avoid inclusion of obvious paratypes. These are specimens cited with the original description, but they are not duplicates of the holotype. Mostly paratypes do, indeed, represent the same taxon as the holotype or lectotype. They are the next most important elements in typification; but sometimes they represent extraneous materials, and might belong to quite different taxa. The main reason for not citing them here involves the endless listing of specimens. They are very numerous, and will be most important to those undertaking revisions and monographs.

Information has been gathered from examination of type collections at the U.S. National Museum (US, 500+); Rocky Mountain Herbarium (RM, 150+); California Academy of Science (CAS, 120+); New York Botanical Garden (NY, 550+); Rancho Santa Ana (POM, 240+); Iowa State University (ISC, ca 100); University of Utah (UT, 100+); Utah State University (UTC, 150+) and Brigham Young University (BRY, 250+). Only selected material has been examined from Gray Herbarium (GH), Carnegie Museum (CM), University of California, Berkeley (UC), Notre Dame University (NDG), and Missouri Botanical Garden (MO). Information on types at the Greene Herbarium at Notre Dame University was taken from a computer printout provided through the generosity of Professor Theodore J. Crovello. Literature has been reviewed for most of the citations, but some have been unavailable. Other citations still await procedures entailed through interlibrary loans.

Type locality information has been abbreviated in some instances to conform to the computer format. Localities of deposition, or supposed deposition, are indicated by the standard abbreviations. Where I have seen the type, the abbreviation is followed by an exclamation mark (e.g., US!). Where the abbreviation stands alone, the place of deposition is taken from literature, or from inference with other collections or names published by the same author, but the specimen has not been seen by me.

Although portions of more than two decades have passed since this work was begun, the data are still incomplete for many of the plant names. I apologize for that lack of completeness, and for the many errors that will become apparent as one uses the list. Some of the problems are apparently insoluble. Plant collectors and authors seldom have been instilled with sufficient foresight to supply all the information necessary for adequate intrepretation of specimens, localities, dates, and other data. Brevity was considered to be a virtue by the collectors (along with an almost impossible, if unstated, belief that others would know what they knew), even when that brevity left out such information as state, locality within the state (or territory), political subdivision of the state, and any other data. Herbarium labels are the sources of information provided by plant collectors, and they should have contained certain basic data. Some of the deficiency, such as lack of place names and surveys, is not the fault of the early workers. Boundaries of the state or territory of Utah were unknown until long after the final reduction of the original Territory of Deseret to its present size in 1868. When one went south from St. George, he was never quite sure when he had entered into Arizona. There is little excuse, however, for the Palmer and Parry labels with only "Southern Utah, Northern Arizona, &c." or "Southern Utah, &c." as the only locality data. In some instances the localities were known only to the collectors, whose passing has denied us of the possibility of ever knowing.

Even when data were provided on labels, the author who subsequently published the name of the plant often failed to cite it. Many of the early publications, and some of the later ones, convey little in the way of accurate data on collector, number, date, locality, or place of deposition of the specimens. Some specimens were taken by obscure collectors, and the locality of collection, dates, and other information remains in doubt.

Localities and dates for some of the plant names have been interpolated by reference with other collections. This is especially the case with county designations; boundaries have changed and new counties have been created since the earliest collections were made, and early collectors were not sure which county they were working in when some collections were made. Some pioneer towns and villages have passed into history, and others have undergone name changes. Present knowledge of distribution allows for accurate placement, at least to county level, of some materials which were provided with vague or misleading locality information.

Problems associated with collections of certain individuals will be discussed in the historical review presented below.

It is believed that the shortfalls in data do not obscure the basic picture of plant exploration in Utah or of the story of publication of taxa based on Utah types. This attempt at analysis of type data in no way detracts from the larger scene of plant studies which resulted from the naming of plants based on types from other areas. The flora of Utah is replete with names of plants with circumboreal and other extra Utah representation dating to 18th- and early 19th-century collectors and authors.

Acknowledged also are the contributions to botany of workers whose main thrust did not include classical taxonomy. Numerous botanists have contributed in ecology, physiology, anatomy, morphology, genetics, and other sophisticated fields of endeavor. Each of those areas has allowed for a greater understanding of the taxonomy of the state. Some investigators contributed to more than one of the major botanical disciplines, or to taxonomy of nonvascular plants, not treated herein. Their exclusion from the lists of collectors and authors, or their low placement in the lists does not imply that the contributions are not great. The measure herein is based on contributions in the strictly classical sense. Neither should naming and description of plants be expected to continue indefinitely. But, the botany of the state is not yet elucidated, and much further work is indicated. This work should not be thought of as representing the final word; certainly many citations of Utah types have been overlooked.

COLLECTORS OF UTAH TYPES

The number of vascular plant types reported for Utah between 1840 and 1981 is approximately 1073. Exact numbers are impossible due to such equivocal label data as "Southern Utah, Northern Arizona, &c." for some collections. The total number that might be in error is thought to be small, and for the purposes of this paper they seem not to affect the overall picture. The types have been taken by 144 collectors acting singly or in combination with one or more collaborators (Table 1). Possibly other collectors are obscured by citations where collection data are lacking. Authors include some 167 individuals acting singly or in combination, and will be discussed later.

A summary of collections of Utah plant types by decade is presented in Table 2.

Earliest types taken from Utah were apparently those by John Charles Fremont in 1843 [*Perchiton occidentale* Torr. & Frem. = *Atriplex canescens* (Pursh) Nutt.] on his first expedition in the American West, wherein he explored the vicinity of the Great Salt Lake. The types of *Gilia stenothyrsa* T. & G. and *Senecio multilobatus* T. & G. were collected by Fremont apparently during 1845 in the Uinta Basin. The 1850s were marked by the efforts of Captain Howard Stansbury, F. Creutzfeldt, Henry Engelmann, and Edward Griffin Beckwith. Stansbury explored the Great Salt Lake in 1850; Creutzfeldt and Beckwith were associated with the ill-fated Gunnison expedition of 1853-54. Creutzfeldt was the botanist for the expedition, whose duty was to survey a route for a railroad to the Pacific (Beckwith 1854), and he was killed along with John Williams Gunnison and most of the others of the party in an ambush by Indians near Delta on 26 October 1853. Beckwith, who was leading another portion of the expedition at the time of the disaster, was named to succeed Gunnison. Creutzfeldt had collected types of two

TABLE 1. Collectors of Utah plant types.

Collectors	Number of types	Years active
Al-Shehbaz, I.A. (b.?)	1	1969
Atwood, N.D. (b.1938)	3	1970–76
Atwood, N.D. (b.1938) & L.C. Higgins (b.1936)	2	1969–73
Atwood, N.D. (b.1938) et al.	1	1971
Bailey, V.O. (1864–1982)	1	1891
Baker, J.G.(1834–1920)	2	1895
Baker, M.S. (1868–1961)	1	1936
Ball, C.R. (1873–1958)	1	1908
Barkley, F.A. (b.?) & M.J. Reed (b.?)	1	1939
Barneby, R.C. (b.1911)	5	1956–66
Beck, D E. (1906–1967)	1	1938
Beckwith, E.G. (1818–1881)	4	1854
Benson, L.D. (b.1909)	4	1948–49
Bishop, F.M. (1843–1933)	4	1872–73
Brandegee, T.S. (1843–1925)	2	1873–75
Burke, M. (b.?)	1	1932
Carlton, E.C. (b.?) & A.O. Garrett (1870–1948)	3	1905
Carrington, J. (b.?)	2	1857
Carter	1	1938
Clawson	2	1935
Clover, E.U. (b.1897)	1	1940
Clover, E.U. (b.1897) & M.L. Jotter (b.1914)	1	1940
Clute, W.N. (b.1869)	1	1919
Cottam, W.P. (b.1894)	8	1929–37
Coville, F.V. (1867–1937) & I.T. Tidestrom (1864–1956)	1	1908
Creutzfeldt, F. (d.1853)	2	1853
Cronquist, A.J. (b.1919)	4	1961
Despain, K. (b.1947)	1	1978
Eastwood, A. (1859–1953)	36	1892–1941
Eastwood, A. (1859–1953) & J.T. Howell (b.1903)	9	1933–41
Eaton, D.C. (1834–1895)	3	1869
Eggleston, W.W. (1863–1935)	1	1912
Ehrendorfer, F. (b.1927) & H.C. Stutz(b.1918)	1	1959
Engelmann, H. (1831–1899)	1	1859
Fallas	1	1928
Ferguson & A.M. Ottley (b.1882)	1	?
Flowers, S. (1900–1968)	1	1933
Fremont, J.C. (1813–1890)	4	1843–45
Garrett, A.O. (1870–1948)	25	1894–1940
Gentry, J.L. (b.?)	1	1968
Gilbert, G.K. (1843–1916)	1	1901
Goodding, L.N. (b.1880)	21	1902
Goodman, G.J. (b.1904) & C.L. Hitchcock (b.1902)	3	1930
Goodrich, S. (b.1943)	2	1980
Gould, F.W. (b.1913)	1	1941
Graham, E.H. (b.1902)	6	1935–37
Hamilton, J.W. (b.?) & O.A. Beath (b.1884)	1	1952
Hanson, C.A. (b.1935)	3	1960–61
Harkness, S.J. (b.?)	1	1902
Harrison, B.F. (b.1908)	2	1939–50
Heil, K.D. (b.1941)	2	?
Hermann, F.J. (b.1906)	3	1933
Hermann, A. (b.?)	1	1953
Higgins, L.C. (b.1936)	3	1968
Hitchcock, C.L. (b.1902)	1	1949
Holmgren, A.H. (b.1912) et al.	4	1947–74
Holmgren, A.H. (b.1912) & S.S. Tillett (b.?)	1	1953
Holmgren, N.H. (b.1937) et al.	10	1965–79

Table 1 continued.

Collectors	Number of types	Years active
Holmgren, N.H. (b.1937) & P.K. Holmgren (b.1940)	4	1970–78
Holmgren, N.H. (b.1937) & J.L. Reveal (b.1941)	7	1965–69
Huffman	3	1953
Johnson, J.E. (1817–1882)	2	1870
Jones, M.E. (1852–1934)	305	1879–1923
Kearney, T.H. (1874–1956) & H.L. Shantz (1867–1958)	2	1912
Klein, W. (b.?)	1	1959
Kuntze, C.E.O. (1843–1907)	2	1874
Larson	1	1934
Leonard, F.E. (1866–1922)	11	1883–85
Linford, J.H. (b.1863)	9	1897
Maguire, B. (b.1904)	26	1932–47
Maguire, B. (b.1904) & H.L. Blood (b.?)	1	1937
Maguire, B. (b.1904) & A.H. Holmgren (b.1912)	1	1946
Maguire, B. (b.1904) & R. Maguire (b.?)	2	1932
Maguire, B. (b.1904) et al.	4	1936–42
Marsh	3	1945
Mathias, M.E. (b.1906)	2	1929
McKelvey, S.D. (b.1883)	2	1934
Mulford, A.I. (b.?)	3	1898
Neese, E. (b.1934) & S. Peterson (b.?)	1	1978
Neese, E. (b.1934) & S.L. Welsh (b.1928)	1	1979
Neese, E. (b.1934) & S. White (b.1955)	1	1977
Nelson, A. (1859–1952)	4	1922
Newberry, J.S. (1822–1892)	2	1959
Nord & Sargent	1	1927
Osterhout, G.E. (1858–1937)	1	1925
Ostler, W.K. (b.1951) & D.C. Anderson (b.1948)	1	1978
Ownbey, G.B. (b.1916)	1	1954
Palmer, E. (1831–1911)	58	1870–77
Pammel, L.H. (1862–1931) & R.E. Blackwood (b.?)	2	1902
Parry, C.C. (1823–1890)	38	1874
Payson, E.B. (1893–1927)	5	1914–26
Peabody, F.J. (b.1948)	1	1976
Pennell, F.W. (1886–1952)	1	1915
Pilsbry	1	1925
Plummer, P. (b.1911)	1	1939
Porter, C.L. (b.1889)	3	1939–50
Purpus, C.A. (1851–1941)	4	1897–99
Reading	1	?
Reveal, J.L. (b.1941)	3	1964–74
Reveal, J.L. (b.1941) & G. Davidse (b.?)	3	1967
Reveal, J.L. (b.1941) & N.H. Holmgren (b.1937)	1	1964
Reveal, J.L. (b.1941) & C. Reveal (b.?)	3	1967–75

Table 1 continued.

Collectors	Number of types	Years active
Reveal, J.L. (b.1941) & S.L. Welsh (b.1928)	1	1966
Ricker, P.L (1878–1973)	1	1917
Ripley, H.D.D. (b.?) & R.C. Barneby (b.1911)	11	1942–47
Rollins, R.C. (b.1911)	7	1937–79
Rollins, R.C. (b.1911) & T.S. Chambers (b.?)	1	1938
Rydberg, P.A. (1860–1931)	8	1895–1911
Rydberg, P.A. (1860–1931) & E.C. Carlton (b.?)	22	1905
Rydberg, P.A. (1860–1931) & A.O. Garrett (1870–1948)	24	1911–13
Sampson, A.W. (b.1884)	1	?
Shands, W.A.	1	1931
Shultz, L. (b.1946) & J. Shultz (b.?)	1	1980
Siler, A.L. (1824–1898)	6	1873–75
Smith, C.P. (1877–1955)	6	1909–25
Stansbury, H. (1806–1853)	11	1850
Stanton, W.D. (b.1900)	2	1930–32
Stokes, S.G. (1868–1954)	4	1900–34
Stoutamire, W.P. (b.?)	1	1957
Thompson, E.L.P. (b.?d.?)	15	1872
Tidestrom, I. (1864–1957)	13	1901–19
Tompkins, P.W. (b.?)	1	1939
Tracy, S.M. (1845–1922)	3	1887–91
Tracy, S.M. (1845–1922) & Evans	1	1887
Trelease, W. (1857–1945)	1	1889
Vicker	1	1901
Walker, E.B. (b.?)	5	1912
Ward, L.F. (1841–1913)	30	1875
Warner, L. (b.?)	1	1957
Watson, S. (1826–1892)	100	1869
Watson, T.J. (b.?)	1	1971
Welsh, S.L. (b.1928)	12	1966–80
Welsh, S.L. (b.1928) & N.D. Atwood (b.1938)	3	1970–72
Welsh, S.L. (b.1928) & G. Moore (b.1917)	2	1963–76
Welsh, S.L. (b.1928) & J.R. Murdock (b.1921)	1	1975
Welsh, S.L. (b.1928) & K.N. Taylor (b.1955)	2	1977
Welsh, S.L. (b.1928) & B.J. Welsh (b.1961)	1	1977
Welsh, S.L. (b.1928) & S.L.T. Welsh (b.1930)	5	1969–75
Welsh, S.L. (b.1928) et al.	5	1969–75
Wetherill, B.A. (1861–1950)	3	1895–97
Wheeler, G.M. (b.1842)	3	1872
Williams, L.O. (b.1908)	1	1932
Winkler	1	?
Woodbury, L.A. (b.?)	1	1977
TOTAL	1073	

Eriogonum taxa in the Green River vicinity. Beckwith took the type of a handsome *Astragalus*, which bears his name. Several taxa were later dedicated to the memory of Gunnison, but unfortunately none of our Utah materials bears the name of Creutzfeldt. Engelmann was meteorologist and botanist with the Simpson expedition (Ewan 1950) and took the type of *Echinocactus whipplei* var. *spinosior* Englemann (named by his brother George Engelmann) somewhere west of Camp Floyd in August 1859.

The first woman collector of Utah types appeared on the scene in the 1850s. Jane Carrington (a Mormon lady) collected some 59 species in the basin of the Great Salt Lake in 1857 (Reveal 1972). She was apparently the first woman to collect plants in the territory since the arrival of the Mormon pioneers, a decade earlier. Two of her collections are the basis of types. They were named by Elias Durand (1860) as *Erysimum asperum* var. *purshii* and *Acerates decumbens*. Perhaps this person is Jane Maria Carrington (26 February 1840, Wiota, Wisconsin), daughter of Albert Carrington and Rhoda Maria Woods, who married Brigham Young, Jr. in March of 1857. Albert Carrington was prominent in early day affairs of the territory of Deseret, serving as editor of the Deseret News (Cooley 1980). Albert Carrington accompanied Stansbury on his exploration of the Great Salt Lake in 1849-50, and would have known of the important plant collections taken by that individual. It seems probable that the collections were taken earlier than the 1857 date indicated, when Jane would have been 15 or 16 years of age.

Table 2. Decade of collection of Utah types, number of collectors,and average number of types per collector.

Decade	Number of Types	Number of Collectors	T/C
1840–49	4	2	2.0
1850–59	23	5	4.4
1860–69	103	2	51.5
1870–79	184	10	18.4
1880–89	54	5	10.6
1890–99	259	9	28.8
1900–09	105	13	8.0
1910–19	60	13	4.5
1920–29	19	9	2.1
1930–39	85	31	2.7
1940–49	46	11	4.1
1950–59	12	11	1.1
1960–69	47	16	2.9
1970–79	52	24	2.2
1980–81	6	2	3.0
Without date	20	4	—
Total	1073	144	7.4

(Note: Because of overlap of collectors into more than one decade, the collectors column totals to more than 144, the actual count of all collectors known for the period.)

The exploration of the region later to be circumscribed as Utah was slow. The 1860s was a quiescent period until its final year. In 1869 Sereno Watson arrived on the scene, accompanied for at least a part of the period by Daniel Cady Eaton (Ewan 1950). The quiescence of the earlier part of the decade was shattered by the advent of these two, especially by the former. They took some 103 types from the state in that year. Mainly they collected in the Wasatch Mountains of Salt Lake, Summit, and Utah counties. Watson visited the Uinta Mountains and islands of Great Salt Lake in the summer of 1869, and he was in the Raft River Mountains in the northwest during 1868. Eaton evidently accompanied him into Provo Canyon, where they collected the type of the beautiful scarlet penstemon which was to bear Eaton's name. Watson was associated with the King' survey of the 40th parallel, and he was its principal botanist (Watson 1871). Despite the apparent paucity of their assault on the unknown plant taxa of the state, Watson and Eaton yielded a huge assemblage of materials, and averaged some 51.5 Utah plant taxa per collector. That figure stands as the all-time high in the history of plant collection in Utah.

Specimens cited as vouchers for taxa reported by Watson and Eaton are numbered in a sequence that corresponds to the species number in the report of the expedition (Watson 1871). Because of this practice, the same number will often include specimens from widely disparate localities, i.e., "East Humboldt Mts., Nevada and Uinta Mts., Utah." When it has been possible to determine that the Utah portion has been selected as lectotype, I have cited that as the type, but when the lectotype has been selected from Nevada, I have excluded that name from among our Utah types. Some of the names cited in the checklist might be in error. They are included here for the sake of completeness.

This same problem exists with collections by Edward Palmer and Charles Christopher

Parry, whose collections were taken astride the Utah-Arizona border, which was not surveyed until later.

Collectors in the 1870s include Joseph Ellis Johnson, Edward Palmer, Mrs. Ellen Powell Thompson (sister of John Wesley Powell), Lt. George Montague Wheeler, Captain Francis Marion Bishop, Charles Christopher Parry, Lester Frank Ward, and finally, in 1879, Marcus Eugene Jones, whose appearance on the scene presaged a lifetime as resident botanist. Jones was to dominate Utah plant taxonomy until 1923, a total of 44 years. Palmer and Parry concentrated their efforts in southwestern Utah, especially in what is now Washington County. Palmer visited the area twice, in 1870 and 1877, and took a total of 58 specimens later designated as types. He was a collector only, depending on others to name the plants he sampled in Utah. Type collections taken by Parry were mainly from his 1874 trip. Parry was in central Utah in 1875, and again in 1877 (with Palmer) at St. George, but these trips added little to his type list for Utah. The total number of his types is 38, and he was responsible for publishing at least 2 of those. According to Jones (Contr. W. Bot. 17: 3. 1930), Parry was in the St. George vicinity for only about a month. His herbarium is at Iowa State University, and contains numerous collections by Palmer along with his own materials (Gabel 1981).

Charles Christopher Parry was born in Admington, Gloucestershire, England, 28 August 1823, and died at Davenport, Iowa, 20 February 1890. He moved with his family to America in 1832, where they settled in Washington County, New York. He received the degree of Doctor of Medicine from Columbia College in 1846, where he was influenced by Dr. John Torrey, professor at that institution (Preston 1897, Gabel 1981). Parry moved to Davenport, Iowa, in 1846. He practiced medicine for a few months only before turning to his greater interest of botany. Following a career exploring the West with various governmental surveys, the pursuit of natural history led Parry to Utah. He came to Utah on a private trip, not associated with any of the surveys.

Contrary to Jones's statement (see above), Parry was in St. George from early April to June of 1874, and then moved north to Cedar City and Beaver. His host in St. George was Joseph Ellis Johnson (Jones 1930, personal correspondence of Parry ISC), pioneer publisher, herbalist, and horticulturalist (Chamberlain 1950). The following year Parry worked out of Spring Lake (Utah County), where he was the guest of Benjamin Franklin Johnson, brother of Joseph Ellis Johnson. His objective for that year was to obtain a collection of the flora in the vicinity of Mt. Nebo, whose flora he decided was depauperate (Parry 1878, Ewan 1950). Parry was an acquaintance of Asa Gray, John Torrey, and George Engelmann. He corresponded with each of them and sent his specimens to them for determination and naming. His contributions to the understanding of Utah plants are significant.

Edward Palmer was born at Wilton, County Norfolk, England on 12 January 1831 and died on 10 April 1911 in Washington, D.C. (McVaugh 1956). He came to America in 1849 where he settled in Cleveland, Ohio. After attending classes at Homeopathic College in Cleveland for a few months during the winter of 1856-57, Palmer moved to Highland, Kansas—to practice medicine. He assumed the title of doctor, which he was to carry the remainder of his life. Previously he had been on an expedition to South America,

Fig. 1. Marcus Eugene Jones (1897), principal pioneer plant taxonomist in Utah (photo courtesy of the Jones family archivist, Charles Walker).

and was soon involved in other expeditions where he collected plant, animal, and archeological materials. In 1870 he arrived by rail at Salt Lake City, where he heard a speech by Brigham Young, was introduced to him, and left for southwestern Utah carrying a letter of introduction provided by Brigham Young. He stayed in St. George and vicinity for about 10 days prior to departing with a party delivering a threshing machine to St. Thomas, Nevada. They left St. George on 17 June 1870, and spent at least a day and a half beyond that date still in Utah. He noted the grand sight of the Joshua tree forest on the Beaverdam Slope. His total collections in Utah for that year is thought to be very small, for he took only about 200 plants total for the latter part of 1869 and all of 1870 (McVaugh 1956). Only seven of the 58 Utah types taken by him were collected in 1870.

Palmer was an acquaintance of C. C. Parry, and Parry helped with distribution of the Palmer material. In 1876 Palmer was employed by the Peabody Museum to do some archeological excavations in southern Utah. He was at St. George from December 1876 to June of 1877. During June he moved his base of operations to Red Creek (Paragonah) where he worked in Bear Valley in early July, then on to Beaver, and finally to Spring Lake. The number of plants taken in Utah in 1877 numbered around 500 (McVaugh 1956), and it was from this series that the bulk of his Utah types were named. Palmer depended on others to name his plants.

Mrs. Thompson, Captain Bishop, and Lester Ward were associated with the Powell surveys of the early-day geological survey. They worked in southwestern, south central, and central Utah. Mrs. Thompson lived for a while at Kanab in 1872, and her collections are from that period. Bishop's collections are from 1872 and 1873, but with little if any provenience data. Some materials credited to Mrs. Thompson obviously came from some distance away from Kanab and were probably taken by members of the Powell survey, including her husband, Almon Harris Thompson.

Bishop was born in New York. He enlisted in the Union army at the age of 17. He was made second lieutenant at the battle of Bull Run first lieutenant at the battle of Antietam, and he was badly wounded at the battle of Fredericksburg. He was discharged with the rank of captain, a title which he carried for the remainder of his life. After the war he attended Illinois Wesleyan University, where one of his instructors was Major John Wesley Powell, whose second expedition he joined as topographer. Following his work with the Powell survey, Bishop joined the faculty of the University of Deseret as professor of science in 1873, where he served until 1877 (Chamberlain 1950). The delicately beautiful *Astragalus episcopus* Wats. is named in his honor.

Ward evidently centered his efforts in the vicinity of the Aquarius Plateau and Rabbit Valley, working out of the hamlet of Glenwood, Sevier County. The handsome milkvetch with diaphanous inflated pods, *Astragalus wardii*, was named in his honor by Gray, and the beautiful low twinpod, *Lesquerella wardii*, was named by Watson. His locality information is much better than provided by any of his contemporaries, bu tthere has been evident confusion asssociated with his labels (Pennell 1920). He was a man of many interests, with expertise in geology, paleobotany, botany, and sociology. Ward published papers in all of those subjects. For a time he was a clerk and librarian at the U.S. Bureau of Statistics. His collections in Utah are from the vicinity of Glenwood, Twelve Mile Canyon, Rabbit Valley, Dirty Devil River, The Button, and Aquarius Plateau (Ewan 1950).

Others who collected type materials in Utah in the 1870s were Lt. George M. Wheeler, Andrew Lafayette Siler, and Townshend Stith Brandegee. The collections of Wheeler are treated, at least in part, in his publication in the United States Geographical Surveys west of the 100th Meridian (Wheeler 1878). Wheeler had little sense of history, as indicated in the total lack of geographical information about plants he collected. Apparently he took some plants in Salt Lake County, as indicated in a letter by Marcus E. Jones, dated "8. 1. 1904" (on file at BRY), in which he intimated that Wheeler, too, had collected *Collomia debilis* in Salt Lake County, but without recording the locality. Brandegee worked with one of the government surveys, mainly in present-day San Juan

County. Siler, a Mormon rancher, lived at a place called "Ranch" near Kanab and took specimens in Kane and adjacent Mohave (in Arizona) counties. He was much interested in cacti and sent a collection of a low depressed-hemispheric ball-cactus to Engelmann, which was later named by Britton and Rose as *Utahia sileri*. Jones (Contr. W. Bot. 16: 46–47. 1930) says of Siler: "He was about seven feet tall, and slim as a rail, and wore about a No. 14 shoe. He was awkward and uncouth, but a real man." Unfortunately, the type of the genus commemorating the state of Utah was collected in the vicinity of Pipe Springs, in Arizona, and that generic name is now synonymized within an expanded *Pediocactus*. Siler's collections are mainly at GH and MO (Ewan 1950).

The 1880s were relatively quiescent when compared to the efforts and successes recorded in the statistics of the 1870s. Together, M. E. Jones, Fred Eugene Leonard, Samuel Mills Tracy (alone and with someone named Evans), and William Trelease collected some 54 types. Jones worked in Washington County in 1880, and widely in Utah in later years of the decade. Leonard took specimens in northern Utah, especially in Salt Lake County. His collections were sent east, where they were named later by Rydberg. William Trelease stopped briefly at Helper in 1889, in transit to St. Louis, Missouri, after spending the summer with the Harriman Alaska Expedition. He collected the type of a yucca that he named in honor of Mrs. Harriman.

Jones moved to Utah in 1880, to Salt Lake City, where he was to reside until 1923. At first he taught in the old Salt Lake Academy, a congregational school. From 1881 to 1885 he conducted a private high school. He was one of the early members of the Utah Natural History Society, of which he was president in 1899, and a fellow of the AAAS. Jones was curator of the museum and librarian at the University of Utah for the year 1889–90. His large herbarium of western plants was stored for a time at the University of Utah (Chamberlain 1950), and it was from there that the collection was retrieved by Dr. P. A. Munz and taken to Pomona College in the 1920s (Richard Shaw, personal communication 1982).

The greatest era for collection of Utah plant types occurred in the 1890s. Marcus E. Jones was the main contributor of type materials. Of the 259 types taken during the decade, Jones was responsible for 193 of them. Jones was employed in 1894 by the U.S. Department of Agriculture as "Special Field Agent" (Jones 1895). He was able to spend the entire field season collecting plants. According to his own account (see Leafl. W. Bot. 10: 208–217. 1965), Jones outfitted a team and buggy that he sent south in early March with a young man as driver. The driver and outfit proceeded to Holden, where they were trapped by a late winter storm. Jones traveled by train to Oasis, where he hired a team and reached Holden in a blizzard. Jones's account is as follows: "The next morning we drove out into the snow and toiled all day in a cloudless sky with the sun dazzling in our faces and by night our faces were burnt to a blister and the serum was oozing off our chins. That night we camped on the desert in a foot of spotless snow where there was hardly enough brush to make a fire and no water but snow. A better bed I never slept

Fig. 2. Alice Eastwood and John Thomas Howell (1936), near Yakima Park, Mt. Ranier, contributors to understanding of botany in Utah and the West (photo by Edith Hardin English, courtesy of John Thomas Howell).

on. The next morning it was bitterly cold to get out of bed and get a fire started in that snow, but warm tea soon thawed us out. That night we slept in mud near Black Rock and the next day were at Milford. Our faces were now all scabs and sores and we looked as though we were suffering from some loathsome disease." Jones was to be in the field, except for short pauses in Salt Lake City, until the 18th of October. During the 1894 field season he collected in Washington, Kane, Garfield, Piute, Sevier, Emery, Carbon (then a part of Emery County), Utah, Sanpete, and Wayne counties. His collections amounted to 4060 numbers, a total of about 35,000 specimens. Never again would anyone have such an opportunity.

The next most important collector of the decade was Alice Eastwood. Born in Canada in 1859, she moved to Denver, Colorado, in 1880, where she taught high school for several years. She was able to devote her life to the study of plants by living initially on the proceeds gained through investment. In 1892 she traveled from Thompson's Springs (present day Thompson) in Grand County south to San Juan County. A second trip was undertaken from Mancos, Colorado, west to Willow Creek in San Juan County, Utah, in the summer of 1895. These trips allowed her access to some of the most remote and rugged country in the southeastern portion of the state. She was able to collect numerous plants on both occasions, among them the types of some of our most unusual plant taxa. Her interest in the region was to continue until her death in 1953 a t the age of 94. Her final trip to the state (with John Thomas Howell) was in 1941. Type collections taken by her in Utah span 50 years, longer than for any other contributor. On at leas t the 1895 expedition she was accompanied by B. Alfred Wetherill, famous for his part in the discovery of the Pueblo dwellings at Mesa Verde, and later pioneer archaeologist in the region. He was to send some few things to Miss Eastwood, and this accounts for his inclusion on the list of Utah plant type collectors.

Fig. 3. John Torrey (1868), author with John Charles Fremont and Asa Gray of specimens taken in Utah by Fremont and by Captain Howard Stansbury, teacher of Charles Christopher Parry, and correspondent of Parry, Palmer, and others (photo courtesy of Richard W. Pohl).

Two other important figures in Utah plant taxomomy appear among the cast of collectors in the 1890s. They are Per Axel Rydberg, a young immigrant from Westergoethland, Sweden, and Aven Nelson, natural history professor at the infant University of Wyoming. Rydberg had arrived in the United States in 1882 and was about to complete his doctorate at the University of Nebraska, where he wrote a conservative treatment of the Rosales of Nebraska. Later he would contribute numerous critical publications of the Rocky Mountain flora, and would have an overwhelming role in the botany of the West. His trip to Utah in 1895 seems not to have been long, and he picked only a few things, mainly in the vicinity of Logan. More will be said of him in later parts of this paper. Nelson had only recently arrived at Laramie (in 1887), where he had accepted a position to teach English, but upon his arrival there found that another English teacher had been hired. He was offered the chair in natural history instead, and was to contribute to knowledge of western American botany for more than five decades.

Completing the list of collectors of types for the decade were Carl Albert Purpus (a German), James Henry Linford (a Utah native), and A. Isabel Mulford, a student of William Trelease at the Missouri Botanical Garden (Ewan 1950). Purpus collected in the La Sal Mountains and in southwestern Utah. Linford's collections are from the northern

Wasatch Mountains, chiefly from Logan Canyon, and the place of deposition is unknown. Mulford traveled through the central and northern regions.

The period from 1900 to 1909 was marked by a decline in types collected. The total number taken was 105, a large number by modern standards, but low when compared to the previous decade. Too, the number of contributors increased. Jones continued to be active, but what does one do for an encore following such a performance as his of the 1890s? Jones took only 17 types, and Rydberg (alone or with Carlton) accounted for 24 types. That Jones was active is indicated by his collections, which yielded type materials for the years 1900, 1903, 1906, 1908, and 1909. Rydberg's contributions were taken in 1905 from Salt Lake County and from the Tushar Mountains, astride the Piute-Beaver counties boundary. The other most important collectors of this time, as regards historical perspective, include Ivar Tidestrom, who was to publish a flora of Utah and Nevada, and Albert Osbun Garrett, resident Utah botanist and teacher for more than four decades. Susan Stokes (who later treated *Eriogonum*), Grove Karl Gilbert (?), Leslie Newton Goodding (student of Aven Nelson), Louis Hermann Pammel and R. E. Blackwood, S. J. (?) Harkness, Frederick Vernon Coville (along with Tidestrom), Carleton Roy Ball (of willow fame), and Charles Piper Smith (producer of infamous works in *Lupinus*) each contributed one or more types during the decade.

The 60 types taken from 1910 to 1919 represented a further decline, emphasized even more by the efforts of 13 collectors for this period. Rydberg, alone and with Albert Osbun Garrett, worked in Salt Lake, Grand, and San Juan counties in 1911. Their work in the southeastern portion of Utah was the first serious attempt at understanding the flora of that region following the pioneer work of Alice Eastwood. Their collections were rich in type materials. C. P. Smith, A. O. Garrett, Willard Webster Eggleston, E. P. Walker, Thomas Henry Kearney and Homer LeRoy Shantz, Edwin Blake Payson, Francis Whittier Pennell, Malmsten, Ricker, and Alice Eastwood provided type material during this time.

The 1920s were a time of transition. Utah was involved in the consequences resulting from World War I, and the field botanists of the early part of the century were involved in activities that did not include active field investigations. Jones sold his collection to Pomona College in 1923 and left Utah for California, where he resided until his death in 1934. Rydberg was involved in completion of parts of the North American Flora and was to pass from the scene upon his death in 1931. The scenario shifted from these actors, who had played such important roles in discovery, to others, most of whom did not occupy the stage for any lengthy period. Only 19 types were added by nine collectors. Jones took his last in 1923, in Zion Canyon, returning to the region of his early pursuits in his old age. A. O. Garrett continued to add specimens during the period. His contributions have never received the meritorious notice that they deserved, although the herbarium at the University of Utah bears his name. Although Garrett founded an herbarium at East High School in Salt Lake City in 1903, his private collection resides at the University of Utah, to which it was given under terms of a bequest following his death in 1948. It is the best early collection extant in Utah.

Walter Pace Cottam entered the botanical scene in the 1920s. He graduated from Brigham Young University with a Master of Science degree in 1917 (the first awarded by the university). He returned to the university as a professor in the early part of the 1920s and began a lifetime investigating the state of Utah. His primary emphasis did not lie with plant taxonomy; he is known for his work in plant ecology. Plants were contributed to the herbarium of Brigham Young University as a biproduct of his investigations of the ecology of the region. He inspired others to follow him into the field and, in fact, has served as an inspiration to generations of scholars. In 1931 he joined the University of Utah and served to found that herbarium also. His early collections are at Brigham Young University and the later ones are at the University of Utah. The herbarium at the University of Utah was founded in 1870 (Chamberlain 1950), prior to Cottam's arrival there, but most of the collections had been destroyed, misplaced, or pilfered by that time. He established the herbarium on a permanent basis in 1933. He had founded the herbarium at Brigham Young University in 1923. The Utah State University herbarium was formalized in 1934.

Other collectors during the 1920s were E. B. Payson (botanist at the Uinversity of Wyoming), Charles Piper Smith (professor of botany at Utah State during the period 1909-12, Ewan 1950), Pilsbry, George Everett Osterhout (amateur botanist and lumberman, whose herbarium is at RM), Nord & Sargent, Fallas, and Mildred Esther Mathias. Payson worked on revisions of genera important in our flora, i.e., *Thelypodium* and its relatives and *Cryptantha* (as *Oreocarya*). Mildred E. Mathias treated the complex and difficult genera in the Umbelliferae.

With Rydberg and Jones both gone from the scene, the 1930s became a time for reevaluation of western American plant taxonomy. The divergent views of taxonomy as exemplified by them were put to the test by no less than 30 individuals who worked in Utah in the decade. Some of these, William D. Stanton (a student of Cottam who worked on the flora of the Henry Mountains), A. O. Garrett, Bassett Maguire, Edward H. Graham, Bertrand F. Harrison, Sevile Flowers, and Perry Plummer, made concerted efforts at continuing the exploration of the state. Others were mainly involved in summary revisions and monographs of plant genera whose members included Utah as a portion of their ranges. Within this category were George Goodman, Charles Leo Hitchcock, Mildred Mathias, Louis Otho Williams, Frederick Joseph Hermann, Alice Eastwood and John Thomas Howell, Susan Stokes, E. B. Payson, Howard Baker, Reed Clark Rollins, Cedric Lambert Porter (curator of the herbariumn at RM for many years), and Susan Delano McKelvey. Minor contributions were made by collectors named Larson, Clawson, Carter, F. A. Barkley and M. J. Reed, and Tompkins.

There occurred a shift within the state during the 1930s. Bassett Maguire had arrived as plant taxonomist at Utah State University (then Utah State Agricultural College) in 1929. Maguire was the first professional plant taxonomist to be employed on a continuing basis by any of the major universities, at least as far as vascular plants were concerned. He was an enthusiastic collector and teacher. His collections within Utah and the surrounding states formed the basis of the herbarium at Utah State. That herbarium became the center of plant taxonomy in Utah in the 1930s under Maguire's direction, and continued to hold that status under his student and successor, Arthur H. Holmgren.

The herbarium at Brigham Young University came under the direction of Bertrand F. Harrison following Cottam's move to Salt Lake City. Harrison was trained in plant physiology, but continued to build the herbarium throughout his tenure at Provo. This was accomplished during a time when he served as chairman of the department of botany, taught 15–25 hours of classes per week (in all botanical disciplines), and functioned on university committees. His favorite class was plant taxonomy, and he instilled the same kind of enthusiasm in his students that he had experienced under the direction of Cottam, who had taught him taxonomy in the 1920s. Slow was the growth of the collection in this period of economic depression and difficulties of travel in the remote regions of Utah. Nevertheless, both Harrison and Cottam were able to contribute substantially to the understanding of the flora and its ecology.

The work of Maguire and his associates clearly places Utah State at the center of taxonomic study in Utah during the 1940s. Maguire, Holmgren, and C. L. Hitchcock (with whom Maguire collaborated), formed a nucleus about which Utah taxonomy functioned. Other workers, all from outside Utah, collected in the state in the decade. Elzada Clover and Lois Jotter traversed Glen Canyon in 1940. Alice Eastwood (then in her 83rd year) and J. T. Howell were in Utah in 1941, allowing Miss Eastwood a final view of the scenes of her earlier explorations. Dwight Ripley and the amazing Rupert Charles Barneby (already working on in his revision of the monumental genus *Astragalus*) visited the state first in 1942. Barneby, an Englishman, with field experience in Spain, where he first encountered the genus *Astragalus*, was inspired to come to North America after seeing the name of *Astragalus asclepiadoides* in a catalogue of North American plants. He then examined the single specimen taken by Jones on deposit at the herbarium at Kew and made the decision that he must see the plant in vivo. Lyman Benson, expert on *Ranunculus* and cacti, was in the state in 1948 and 1949. Frank Gould, specialist in grasses, collected here in 1941. A person named Marsh took materials in both 1945 and 1946.

The 1950s mark a period of quiescence in exploration and collection of Utah plant types. Maguire had left Utah State for the New York Botanical Garden, and the post World War II era found the professors involved with teaching and other pursuits, which did not allow them to allot much time to collecting. Fewer types were taken in this decade than any time since the 1850s. Arthur Hermann Holmgren, B. F. Harrison, C. L. Porter, Rupert C. Barneby, F. J. Hermann, and others contributed only 13 types in the period. The list gives Utah State and Brigham Young about equal, if unimpressive, billing.

Collectors during the 1960s were affiliated with Utah State (Arthur Holmgren, his son Noel Hermann Holmgren , and Garrett Davidse), New York Botanical Garden (Rupert C. Barneby and Johnnnie L. Gentry), and Brigham Young University (Craig Hanson, Stanley Larson Welsh, Glen Moore, James Reveal, Larry Charles Higgins, Stella Leimomi Tree Welsh, and Nephi Duane Atwood). Ishan A. Al-Shebaz (of Harvard University) was the only other collector of Utah plant types in the decade. Personnel from Utah State and New York Botanical Garden were engaged in a collaborative study of the intermountain flora preparatory to publication of a manual of that flora. The school that developed at Brigham Young University resulted from the serendipity that followed the acceptance of the position of plant taxonomist (the first for the university) by Welsh in September of 1960. Welsh, his wife, and his students began a concerted effort at exploration of the flora of Utah. The nucleus of the herbarium developed by Cottam and by Harrison allowed for continued expansion as the flora of the state was investigated. Exploration and collection produced some 50 specimens that have been named as types at the present.

During the 1970s some 47 type specimens were taken. The essential group of collectors remained largely the same as in the previous decade, but there was some shift in institutional affiliation and new names appeared. Noel and Patricia Kern Holmgren became affiliated with New York Botanical Garden, and James Reveal was employed by the University of Maryland. Leila Shultz joined Arthur Holmgren as curator of the herbarium at Utah State University late in the decade. The roster of people at Brigham Young Universty who aided in collection of type materials include S. L. Welsh, N. D. Atwood, Joseph Richard Murdock, Frederick J. Peabody, Kaye Hugie Thorne, Kathryn N. Taylor, Elizabeth Janet Chase Neese, Susan White, Kent Ostler and David Anderson, Kim Despain, Betty Jean Welsh, and S. L. T. Welsh.

Counties of Collection

An examination of types taken on a per county basis is instructive as to where emphasis was given in early botanical excursions. Data on types by county are presented in Table 3. Washington County was and is a favorite site for investigations by those tired of the cold and snow of winter, and, because of the warm desert vegetation, which reflects its climate, many people traveled there to collect. Palmer, Parry, and Jones were there

Fig. 4. Daniel Cady Eaton (1864), author of the Compositae in Watson's *Botany*, who is honored by the name *Penstemon eatonii* Gray (photo courtesy of Richard W. Pohl).

early, in the 70s and 80s, when many of the taxa were undescribed. Because of their attention to that delightful region for early spring and autumn floras, Washington County stands in first position with 163 types. Salt Lake County is second with 102, in part because of its unique flora that extends from moderate to very high elevations, and in part because of its position within the state. Early taxonomists visited Salt Lake City, center of commerce and hub of transportation for this vast region. Access to the mountainous areas around the valley of the Great Salt Lake was relatively easy for those operating from this base. Jones's visit to the Wasatch Mountains in 1879 yielded many types. Watson, Jones, Rydberg, Garrett, Stokes, and many others spent time in the canyons and ranges in close proximity to Salt Lake City. The large number of types from San Juan and adjacent Grand counties is attributable in large part to the early work by Eastwood and Rydberg and Garrett. Garfield County owes its large compliment of types to the early work by Rydberg, and to later attempts by more recent collectors. Summit County became important in types largely, I believe, because of the access to the westernmost portion of the Uinta Mountains, and especially because of the early trip to the area by Watson.

Table 3. Utah types listed by county of collection.

County	Number
Beaver	25
Box Elder	7
Cache	28
Carbon	21
Daggett	3
Davis	9
Duchesne	19
Emery	45
Garfield	56
Grand	43
Iron	20
Juab	23
Kane	59
Millard	19
Morgan	1
Piute	35
Rich	2
Salt Lake	102
San Juan	85
Sanpete	22
Sevier	48
Summit	53
Tooele	36
Uintah	33
Utah	30
Wasatch	9
Washington	163
Wayne	26
Weber	4
Unknown	47
Total	1073

Tremendous effort and expense is necessary for exploration of the state. Most of the remaining endemics, if past experience is correct, will be found in areas that remain to be explored in remote parts of the state. Each year a few more are discovered, and with each new generation of monographers additional types will be designated from among collections of the previous years.

AUTHORS OF TAXA BASED ON UTAH TYPES

Those who collect types may or may not be prepared to describe taxa based on them. Indeed, few are those who recognize, immediately upon collection, that the material collected is undescribed. Often, new taxa are made to fit into concepts of previously described entities, whether they fit well or not. Each worker is acquainted with only a portion of the variation of the total flora, and few consider themselves sufficiently prepared to name as new all portions of the variation encountered by them. To some investigators any variation is worthy of a name, regardless of the importance of that characteristic in the total range of variation available. To them the value of a single character is overriding—the character makes the species, as Linnaeus stated. Because of differences in training, philosophy, and expertise, and others due to change in understanding over more than a century of time, the lasting quality of names recognized as belonging to viable entities varies from author to author, and from group to group treated by the same author. There have always been more specialists involved with naming than with collecting. Beacuse of this, many authors never saw the taxa that they named in vivo—they were herbarium botanists with experience in dried and pressed plants only. Among the herbarium botanists quality of judgments varied as much as between them and their field-experienced counterparts. Gray and Watson represent the two extremes, and both were successful descriptive botanists whose named taxa have stood the test of time. The syndrome of "name in print at any cost" afflicted only a few of the major authors (i.e., Edward L. Greene and Charles Piper Smith). The names of authors of Utah types are listed in Table 4. The decade of publication of Utah types, number of authors, and average number of names per author are cited in Table 5.

There has always been a disparity among botanists regarding species concept and application of names. As there has always been a problem of distinguishing between nomenclature and taxonomy, a problem has also existed between botanists in the recognition of species in which infraspecific categories are allowed. Some have chosen to draw species concepts that are broad and allow for the inclusion of several infraspecific taxa in a hierarchial system. Others have felt that such a nested system, in which species, subspecies, varieties, subvarieties, and forms were allowed, represented a return to pre-Linnaean phrase names. To them such usage was and is intolerable; the binomial system of nomenclature should be adhered to at all costs. When this concept is followed, and when it is coupled with the concept that any variant is worthy of a name, it is possible to multiply names inordinately.

Names based on Utah types were supplied by workers from both of the divergent schools, and by others between. Still other workers were not bound by the sense of logic provided by either school; they were self-taught and were trapped in their preconceived notions that any variation constituted a case for a new species, and that the species were immutable. Because of the differences in approach, in understanding, and in training, our Utah plants were given a variety of treatments. The variation among botanists today is not as great, but there is still variation. A current move has been to recognize only one infraspecific category, the subspecies. If such a move were to succeed, then all variants now recognized at other infraspecific levels would be treated as subspecies, and levels of variation would be hidden by the apparent uniformity of the category. It is true, of course, that taxonomy should not be dependent upon nomenclature, but where the disciplines can supplement each other that course seems best to this worker.

Some of the cast of authors is the same as for the list of collectors, but many are different. Noted is the fact that some of the collectors of many types failed to publish new taxa based on their own collections. That task fell to others, either by default or on purpose. One will note that Jones named only 167 taxa but collected some 305. The others were named by some 44 botanists during and subsequent to Jones's lifetime, the latest by Reveal (1977). This was particularly disturbing to Jones, not because others purloined his material, but because he did not feel that most of them were worthy of being named.

The 1840s demonstrate only two authors of Utah taxa, i.e., John Torrey and John Charles Fremont, and John Torrey and Asa Gray. Torrey was situated at Columbia College, New York, and Fremont was then engaged in explorations of the West. Later, Fremont would be a candidate for the presidency of the United States (in 1856). Together they named *Perchiton occidentale* (Torrey & Fremont 1845). Torrey and Asa Gray collaborated in naming *Gilia stenothyrsa* and *Senecio multilobatus* (Torrey and Gray 1849). All these taxa are based on specimens taken by Fremont. Asa Gray, working out of

Fig. 5. Sereno Watson (ca 1870), collector and author of Utah plant types, second in importance only to Marcus E. Jones (photo courtesy of Richard W. Pohl).

Harvard University, was the principal 19th-century American plant taxonomist; his contributions are legion.

Five authors described taxa based on Utah types in the 1850s. These include John Torrey, Torrey and Gray, Elias Durand, George Bentham, and Edward Griffin Beckwith. Their published taxa are based on collections by Stansbury, Creuzfeldt, Beckwith, and Carrington. Seven of the 12 taxa stand at some taxonomic level in contemporary treatments. Perhaps the best known of the taxa described in the decade is *Phaca mollissima* var. *utahensis* named by Torrey and now cited as *Astragalus utahensis* (Torr.) T. & G. Torrey and Gray were the principal American taxonomists of the period. John Torrey (1796–1873) was a professor at Columbia College. He became associated with Asa Gray (1810–1888), his student, in writing a "Flora of North America" (1838–1840). Gray

TABLE 4. Authors of names of Utah plant types.

Author	Number of names	Years active
Al-Shehbaz, I.A. (b.?)	1	1973
Anderson, L.C. (b.1936)	1	1981
Atwood, N.D. (b.1938)	4	1972–73
Bailey, L.H. (1858–1954)	1	1884
Baker, M.S. (1868–1961)	2	1938–40
Baker, M.S. (1868–1961) & J.C. Clausen (b.1891)	1	1949
Ball, C.R. (1873–1958)	1	1921
Barkley, T.M.(b.1934)	1	1963
Barneby, R.C. (b.1911)	22	1942–66
Barneby, R.C. (b.1911) & N.H. Holmgren (b. 1937)	1	1979
Beal, W.J. (1883–1924)	1	1896
Beaman, J.H. (b.1929)	2	1957
Benson, L.D. (b.1909)	3	1948–69
Bentham, G. (1800–84)	1	1856
Bicknell, E.P. (1859–1925)	1	1901
Blake, S.F. (1892–1959)	7	1922–37
Brand, A. (1863–1930)	9	1907–11
Brandegee, M.K. (1844–1920)	2	1900
Brenckle, J.F. (b.1875) & W.P. Cottam (b.1875)	1	1840
Britton, N.L. (1859–1934)	2	1904–08
Britton, N.L. (1859–1934 & J.N. Rose (1862–1928)	1	1923
Buchenau, F.G.P. (1831–1906)	1	1890
Candolle, A.L.P.P. (1806–93)	1	1864
Chaudhri, M.N. (b.1932)	1	1968
Clover, E.U. (b.1897) & M.L. Jotter (b.1914)	1	1941
Cockerell, T.D.A. (1866–1948)	2	1904
Cottam, W.P. (b.1894)	1	1939
Coulter, J.M. (1851–1928) & J.N. Rose (1862–1928)	8	1888–1910
Coville, F.V. (1867–1937)	3	1892–93
Cronquist, A.J. (b.1919)	9	1943–63
Darlington, J. (b.1905)	1	1934
Daston, J.S. (b.?)	3	1946
Dempster, L.T. (b.1905) & F. Ehrendorfer (b.1927)	2	1965
Durand, E.M. (1794–1873)	2	1860
Earle, W.H. (b.?)	1	1980
Eastwood, A. (1859–1953)	38	1893–1942
Eaton, D.C. (1834–1895)	15	1871
Ehrendorfer, F. (b.1929)	2	1956
Engelmann, G. (1809–84)	13	1871–96
Engler, H.G.A. (1844–1930) & E. Irmscher (1887–1968)	1	1916
Fedde, F.K.G. (1873–1942)	2	1909–13
Flous, M.F. (b?)	1	1934
Flowers, S. (1900–1968)	1	1949
Gandoger, M. (1850–1927)	9	1905–20
Garrett, A.O. (1870–1948)	1	1917
Gates, R.R. (1882–1962)	1	1915
Gentry, J.L. (b.?)	1	1979
Goodding, L.N. (b.1880)	5	1904
Goodman, G.J. (b.1904) & C.L. Hitchcock (b.1902)	1	1932
Gould, F.W. (b.1913)	1	1942
Gray, A. (1810–1888)	65	1852–84
Greene, E.L. (1843–1915)	44	1896–1912
Greenman, J.M. (1867–1951)	5	1914–17
Greenman, J.M. (1867–1951) & E.M. Roush (b.1886)	1	1929
Hackel, E. (1850–1926)	1	1896
Hanson, C.A. (b.1935)	3	1962
Heil, K.D. (b.1941)	3	1979
Heimerl, A. (b.1857)	1	1902
Heiser, C.B. (b.1920)	1	1961
Heller, A.A. (1867–1944)	1	1905
Hermann, F.J. (b.1906)	2	1934–37
Higgins, L.C. (b.1936)	3	1968
Hitchcock, A.S. (1865–1935)	1	1933
Hitchcock, C.L. (b.1902)	6	1941–52
Hitchcock, C.L. (b.1902) & B. Maguire (b.1904)	1	1947
Holm, T.H. (1854–1932)	1	1891
Holmgren, A.H. (b.1912), L.M. Schultz (b.1946), & T.K. Lowrey (b.?)	1	1976
Holmgren, N.H. (b.1937)	8	1973–79
Holmgren, N.H. (b.1937) & A.H. Holmgren (b. 1912)	1	1974
Holmgren, N.H. (b.1937) & P.K. Holmgren	1	1979
Hopkins, M. (b.1906)	1	1937
House, H.D. (1878–1949)	1	1906
Howell, J.T. (b.1903)	4	1940–43
Johnston, I.M. (1898–1960)	6	1923–52
Jones, M.E. (1852–1934)	167	1880–1933

Table 4 continued.

Author	Number of names	Years active
Klein, W. (b.?)	1	1962
Koehne, B.A.E. (1848–1918)	1	1895
Kuntze, C.E.O. (1843–1907)	5	1885–95
Leveille, A.A.H. (1863–1918)	1	1905
Macbride, J.F. (1892–1976)	3	1916
Macbride, J.F. (1892–1976) & E.B. Payson (1893–1927	1	1917
Mackenzie, K.K. (1877–1934)	1	1917
Maguire, B. (b.1904)	18	1941–51
Maguire, B. (b.1904) & A.J. Cronquist (b.1919)	1	1947
Maguire, B. (b.1904) & A.H. Holmgren (b.1912)	1	1946
Maguire, B. (b.1904) & R.E. Woodson (1904–1963)	1	1941
Marshall, W.T.	1	1954
Martin, R.F. (b.1910)	1	1940
Mathias, M.E. (b.1906)	2	1930–32
McKelvey, S.D. (b.1883)	2	1947
Mez, C.C. (1866–1944)	1	1921
Morton, C.V. (1905–1972)	1	1937
Munz, P.A. (1892–1974)	2	1928–31
Murray, E.	1	1980
Neese, E. (b.1934) & S.L. Welsh (b.1928)	1	1981
Nelson, A. (1859–1952)	32	1900–45
Nelson, A. (1859–1952) & J.F. Macbride (1892–1976)	1	1916
Nelson, E.E. (1876–1949)	2	1899–1901
Norton, J.B.S. (1872–1966)	1	1899
Osterhout, G.E. (1858–1937)	1	1926
Ottley, A.M. (b.1882)	1	1944
Ownbey, G.B. (b.1916)	1	1958
Parry, C.C. (1823–1890)	3	1874–75
Payson, E.B. (1893–1927)	5	1915–26
Pennell, F.W. (1886–1952)	17	1920–37
Petrak, F. (1886–1973)	3	1917
Pilger, R.K.F. (1876–1953)	1	1922
Piper, C.V. (1867–1926)	1	1899
Porter, C.L. (b.1905)	3	1952
Purpus, J.A. (1860–1932)	1	1909
Raven, P.H. (b.1936)	2	1962–69
Rechinger, F.	1	1936
Reveal, J.L. (b.1941)	24	1966–77
Reveal, J.L. (b.1941) & J.D. Brotherson (b.1938)	3	1966–68
Robbins, J.W. (1801–1879)	1	1871
Robinson, B.L. (1864–1935)	1	1917
Robinson, B.L. (1864–1935) & J.M. Greenman (1867–1951)	1	1899
Rollins, R.C. (b.1911)	9	1937–81
Rosendal, C.O. (1875–1956), F.K. Butters (1878–1945), & O. Lakela	1	1936
Rydberg, P.A. (1860–1931)	150	1900–29
Schneider, C.K. (1876–1951)	4	1905
Schulz, O.E. (1874–1936)	2	1924–27

Table 4 continued.

Author	Number of names	Years active
Scribner, F.L. (1851–1938)	1	1911
Scribner, F.L. (1874–1938) & T.A. Williams (1865–1900)	1	1899
Sharp, W.M.	1	1935
Sheldon, E.P. (b.1869)	3	1894
Shultz, L. (b.1946) & J. Shultz (b.?)	1	1980
Slosson, M. (b.1873)	1	1914
Small, J.K. (1869–1938)	5	1898–1905
Smiley, F.J. (b.1880)	1	1916
Smith, C.P. (1877–1955)	11	1948–51
Smith, J.G. (1866–1925)	1	1899
Standley, P.C. (1884–1963)	1	1916
Stockwell, W.P. (1898–1950)	1	1940
Stokes, S.G. (1868–1954)	14	1903–36
St. John, H. (b.1892)	1	1915
St.-Yves, A. (1855–1933)	1	1925
Suksdorf, W.N. (1850–1932)	2	1931
Swallen, J.R. (b.1903)	1	1931
Thurber, G. (1821–1890)	1	1871
Tidestrom, I. (1864–1957)	8	1910–14
Torrey, J. (1796–1873)	9	1850–71
Torrey, J. (1796–1873) & J. C. Fremont (1813–1890)	1	1845
Torrey, J. (1796–1873) & A. Gray (1810–1888)	9	1849–70
Trelease, W. (1857–1945)	3	1896–1907
Tuzson, J. (b.1870)	1	1921
Underwood, L.M. (1853–1907)	1	1898
Vasey, G. (1822–1893)	2	1876–93
Voss, J.W. (b.1907)	1	1937
Wagner, W.L.	1	1981
Watson, E.E. (1871–1936)	1	1929
Watson, S. (1826–1892)	88	1871–88
Watson, T.J. (b.?)	1	1977
Weber, W.A. (b.1918)	2	1946
Welsh, S.L. (b.1928)	18	1970–80
Welsh, S.L. (b.1928) & N.D. Atwood (b.1938)	4	1975–81
Welsh, S.L. (b.1928) & R.C. Barneby (b.1911)	1	1981
Welsh, S.L. (b.1928) & S. Goodrich (b.1943)	8	1980–81
Welsh, S.L. (b.1928) & G. Moore (b.1917)	1	1963–68
Welsh, S. L. (b.1928) & E.J. Neese (b.1934)	1	1981
Welsh, S.L. (b.1928) & J.L. Reveal (b.1941)	6	1968–77
Wherry, E.T. (b.1885)	2	1943–44
White, T.G. (1872–1901)	1	1894
Williams, L.O. (b.1908)	4	1932–37
Williams, T.A. (1865–1900)	1	1899
Wooton & Standley	1	?
Yuncker, T.G. (b.1891)	1	1960
TOTAL	1073	

was to be associated with Torrey throughout his life, and in a biography compiled at Torrey's death, Gray (1873) noted that "... he went again across the continent to California, and ... enjoyed the rare pleasure of viewing in their native soil, and plucking with his own hands, many a flower which he had himself named and described from dried specimens in the herbarium, and in which he felt a kind of paternal interest."

The 1860s did not offer much in the way of opportunity for description of Utah plant taxa. Torrey and Gray described *Navarretia setosissima*, and de Candolle named *Quercus stellata* var. *utahensis*, based on a collection presumeably taken by Beckwith "between Salt Lake City and the Sierra Nevada" in 1854.

Sereno Watson and Asa Gray dominated the botanical literature dealing with Utah plant types in the 1870s. They were joined by John Torrey, Daniel Cady Eaton, James Watson Robbins, George Vasey, George Engelmann, Lester Frank Ward, and Charles Christopher Parry in the publication of some 161 taxa. The most important single work of the decade is the report of the U.S. Geological Survey of the 40th Parallel, Volume 5, Botany, authored by Watson (1871), but in collaboration with D. C. Eaton (honored in the name *Penstemon eatonii* Gray), George Engelmann, and J. W. Robbins. The work included 51 taxa based on Utah types (39 by Watson, 10 by Eaton, one by Engelmann, and one by Robbins), mainly collected by Watson and Eaton in 1869. Watson ranks second only to Jones in number of types collected, and is third after Jones and Rydberg in the number of taxa described on the basis of Utah type material.

TABLE 5. Decade of publication of Utah types, number of authors, and average number of names per author.

Decade	Number of names	Number of authors	N/A
1840–49	2	2	1.0
1850–59	14	5	2.8
1860–69	4	3	1.3
1870–79	166	10	16.6
1880–89	27	6	4.5
1890–99	181	24	7.5
1900–09	180	18	10.0
1910–19	145	25	5.8
1920–29	59	19	3.1
1930–39	61	27	2.3
1940–49	75	28	2.7
1950–59	25	11	2.3
1960–69	44	16	2.8
1970–79	56	14	4.0
1980–81	24	12	2.0
Total	1073	167	6.4

The tremendous effort of the 1870s appears to have almost exhausted the botanical authors. The 1880s were, by contrast, relatively quiescent. Only 27 taxa established on Utah plants were named in the period. Gray named 13; Watson only two. The remainder were divided among Vernon Bailey, Otto Kuntze, and John Merle Coulter and Joseph Nelson Rose. Marcus E. Jones sent his early collections taken during this period to Gray and Watson, but when he felt unjustly controlled by their editorship of some eastern journals, Jones bided his time until Gray was dead (in 1888), before beginning to publish in earnest in the 1890s.

If the 1880s were relatively quiet, they were a calm before the storm. The death of Gray in 1888 and of Watson in 1892 allowed for an increase of activity across the West. The removal of these two giants of American taxonomy from the scene coincided with the coming of age of Jones in his exploration of Utah. His species concepts had been obtained from his early training, when Gray's *Manual of Botany* (published in 1867) had influenced him. He had received reinforcement in his concept by early contact with Gray but most especially, from his application of earlier perceived concepts with plants as he found them in the field. Jones, with only a meager contribution in the 1880s, named a staggering 118 taxa from Utah in the 1890s, 75 of them in a single publication (Proc. Calif. Acad. II, Vol. 5. 1895). Jones did not occupy the field alone. Some 24 others authored taxa from among the wealth of undescribed botanical materials. The list of authors includes: Bernard Adalbert Emil Koehne, Franz George Phillipp Bucheneau, Carl Ernst Otto Kuntze, Herman Teodor Holm, Fredrick Vernon Coville, A. Eastwood, George Vasey, Edmund Parry Sheldon, Theodore Greely White, Edward Lee Greene, William James Beal, John Kunkel Small, Eduard Hackel, William Trelease, George Engelmann, Per

Axel Rydberg, Thomas Henry Kearney, Lucien Marcus Underwood, Aven Nelson, Thomas Albert Williams, Benjamin Lincoln Robinson, Jesse Moore Greenman, Jared Gage Smith, Charles Vancouver Piper, and Elias Emanuel Nelson. Alice Eastwood and Per Axel Rydberg were both beginning their activities within Utah; they would spend decades involved, in part, with the Utah flora. The decade was the golden age of descriptive botany in Utah, and in deference to Jones's contributions the decade should be known as the "Jonesian Era."

The decade from 1900 to 1909 showed only a slight decline in taxa named from the state when compared to the previous decade (180 compared to 181), with the deficit in types collected in that period (105) being made up by names being applied to specimens taken previously. Some 18 authors assaulted the collections of the state. Jones did not come close to matching his unparalled feats of the 1890s. He named only 21 taxa in the decade. Rydberg, an enthusiastic and energetic professionally trained botanist, rushed to fill whatever vacuum was left following Jones's valliant efforts. Introduced to the region in the mid-90s, Rydberg had named only one taxon from Utah prior to the turn of the century. Now he assumed the leading position as author of 65 Utah types in the decade, in preparation for publication of his flora of the Rocky Mountains (1917). Principal authors besides Rydberg and Jones were Edward L. Greene (21 names) and Aven Nelson (20 names).

Rydberg had no close competition in the period from 1910 to 1919. He named another 65 taxa based on Utah materials, and Jones named only 14. The 1920s were the lowest for publication of new taxa since the 1880s. Only 59 taxa were named by 19 authors. Rydberg authored only 9, second to F. W. Pennell, then engaged in a revision of the genus *Penstemon*, who named 14 taxa.

Neither Jones nor Rydberg were to live beyond the early 1930s. Jones named a final 4 taxa in that decade. The period fell to Sidney Faye Blake (4), Alice Eastwood (4), Ivan Murray Johnston (2), David Daniels Keck (4), Aven Nelson (2), F. W. Pennell (3), and Susan Gabriella Stokes (12), largely without a leader. Leadership in the naming of Utah's plants in the 1940s clearly belongs to Bassett Maguire, who accepted a position at Utah State Agricultural College in the 1930s. Others working in the flora of the state in the 1940s, who contributed names of new taxa, include Rupert Charles Barneby, Arthur John Cronquist, Alice Eastwood, C. Leo Hitchcock, John Thomas Howell, Ivan M. Johnston, and David D. Keck.

The 1950s were relatively quiet. This period was marked by the shift from efforts of World War II, and Bassett Maguire had left Utah State. Charles Piper Smith, in his senescence, and suffering from a lack of understanding of what constituted a species within *Lupinus*, named seven inconsequential lupines as species, all but one of them from the head of Salina Canyon, and all of those belonging to *Lupinus sericeus* in a broad sense. Barneby named five species during this period.

In the decade of the 60s Barneby (with 9 new taxa) was displaced by James Lauritz Reveal (with 15 new taxa) as leader in authorship of new names. Reveal had begun his assault on *Eriogonum*, a genus rich in endemic taxa and other narrowly restrcted plants. Craig Hansen, James L. Reveal, and Larry

Fig. 6. Asa Gray (ca 1865), author of numerous Utah types, based on collections corresponded by Watson, Parry, Thompson, Siler, Bishop, Palmer, and Jones, and the most important North American plant taxonomist of the 19th century (photo courtesy of Richard W. Pohl).

Charles Higgins and Stanley L. Welsh, all associated with Brigham Young University, named a third of all species described during the decade.

Botanical exploration continued at an accelerated pace in the 1970s. Impetus for publication of the taxa discovered in this period was supplied by preparation of the grand plan for publication of the "Intermountain Flora" by members of New York Botanical Garden and associates. Included in that team are Arthur J. Cronquist, Arthur H. Holmgren, Noel H. Holmgren, Patricia K. Holmgren, and James L. Reveal. Noel Holmgren, alone or in combination with others of the group, published descriptions of 10 new taxa from Utah, and Reveal published 11.

Work on exploration of floristic provinces of Utah by botanists from Brigham Young Universtiy was expanded in the 1960s. and was again intensified in the 1970s. The Utah Flora project, initiated in the 1960s, offered stimulus. Further activity was increased by passage of environmental protection laws, and especially by passage of the Endangered Species Act of 1973, as amended in 1978. Welsh, alone or with others, described 29 taxa in the decade. That is the largest number involving any individual since the 1910–1919 period. Atwood named 4, bringing the total for those at Brigham Young University to 33, or 61 percent of the total for the decade.

THE DECADES BEYOND

That the past is prologue is illustrated by the fact that several new taxa have been described from Utah since the close of the period covered by this text. Those which have been published are included in the list of type material, but they are not summarized as for previous decades. Too, I recognize that a decade does not begin with the zero year, but ends with it. For the sake of convenience on my part, I have chosen to use it otherwise. Those who follow can find fault, as all who view others' work must, but it will not materially affect the data presented here or my view of the history of plant collection in Utah. Perhaps some will find this summary useful, and possibly someone will choose to keep it current for the future.

MARCUS EUGENE JONES—HIS CONTRIBUTIONS AND HIS CONTEMPORARIES

In the summer of 1879 (Broaddus 1935) an event occurred which, because of its happenstance and because of its forthrightness, would not seem to have any lasting effect. A young botanist, on one of his earliest trips west from the rolling farmlands of Iowa, happened to find a wallet (Munz 1965) that belonged to a General Wm. J. Palmer. The wallet contained valuable papers and was returned to its owner. Following this act of an honest man, General Palmer sent the botanist, Marcus E. Jones, on repeated trips to explore regions for mining or agricultural potential. Jones was enabled to travel widely in the western portions of the continent, all because of serendipity—the finding and return of another's property. Because of this, western American plant taxonomy was altered for all time. He indicated his gratitude to Palmer (Jones 1891) by naming *Cleomella palmerana*; "Dedicated to General Wm. J. Palmer, than whom there is no one more interested in scientific researches in Utah, or who has shown more interest in a more substantial way."

Jones was born in Jefferson, Ashtabula County, Ohio, on 25 April 1852 and died at San Bernadino, California, in his 83rd year on 3 June 1934. He was reared and educated near Grinnell, Iowa, having moved west with his family in 1865 ("on the very day that Lincoln was shot"), graduating from Grinnell (Iowa) College in 1875 (Broaddus 1935). In 1876 and 1877 the youthful botanist collected plants in Iowa. Early in 1878 he left for Colorado, where he collected large numbers of specimens that were sold as "sets." He returned to Colorado Springs in 1879 as "professor of natural science." During July he traveled to Salt Lake City and collected at Alta, City Creek Canyon, Lake Point, and Bingham Canyon.

Jones moved from Iowa to establish permanent residence in Salt Lake City in 1880. Accompanying him was his bride (since February 18), Anna Elizabeth Richardson (1853–1916), who would spend most of the remainder of her life with Jones in Salt Lake City. Instructive is his account (Munz 1965) of the itinerary from Salt Lake City to

Washington County and return during the spring of 1880.

"I left Iowa Falls, Iowa, February 18th for Salt Lake City and got there the 24th. March 3rd I hired a team and started to drive to St. George. I reached Sandy. On the 4th I returned to Salt Lake and back to Sandy (having forgotten something). On the 5th reached Pleasant Grove, Spanish Fork on the 6th, Mona on the 8th, and Juab on the 9th, Warm Springs near Gunnison on the 10th, Willow Bend below Richfield on the 11th, Elsinore on the 12th, where I stayed three days and went 14 miles up the Clear Creek Canyon on the 18th. Then went seven miles farther on the 19th, then to Pine Creek fifteen miles above Beaver, Beaver on the 20th, Buckhorn Springs on the 22nd, Summit south of Parowan on the 23rd, then to Fort Hamilton on the 24th where I found the first spring flowers. I reached Leeds on the 25th and St. George on the 26th. I botanized all around the city on the plains and mesas until the 9th of April when I went over on the Santa Clara. On the 14th I went to Washington five miles east. On the 20th I started for Salt Lake and reached Bellevue. On the 21st got to Kararrah (Kanarrah?). On the 22nd Fort Hamilton. On the 23rd Parowan. On the 24th. Beaver. On the 27th Corn Creek. On the 28 Fillmore. On the 29th to the ridge north of Scipio. On the 30th I reached Nephi. On May 1st I reached Spanish Fork. On the 3rd, I reached the Point of the Mountain and the 5th Salt Lake City."

One cannot find in Jones's rather voluminous published writings whether his young and beautiful bride of a few weeks accompanied him on this long and tiring trip. He makes no official acknowledgment that she did go with him. In an account of Anna Jones's life written by her daughter (Broaddus 1952), however, it is noted that "At first Anna went with him on wagon trips of incredible difficulty and danger, even as far as St. George in southern Utah, helping collect wild flower specimens, pressing and drying them, assembling sets for shipment to Ejropean and eastern herbaria, even mounting many of the most attractive flowers in little booklets of 'Western Flora,' which they sold." Probably she was on this first trip south; it is inconceivable to think otherwise. His respect for women was less than overwhelming. Marcus (called Mark by his family and close friends) wrote of his great admiration and love for his mother (Jones and Broaddus 1952), but he demonstrated little regard for other women. His unpublished diary of 1880 (POM) cites his expenses on his wedding day, and then, almost as an afterthought, notes in the margin of the diary, "today I married Anna Elizabeth Richardson."

Anna Jones was a talented and educated woman, having taught school for several years from the age of 16, in Iowa Falls, Iowa, and in the surrounding area. She went to Grinell to complete one year of advanced study in English, but remained to complete the college course. Finally, she accepted a position as "Lady Principal" at Grinell (Iowa) College, a position she resigned in January of 1880 so that she could marry one of her former Latin teachers, Marcus Eugene Jones.

It is evident from correspondence and from the published account of her life that Anna Jones supported her husband in his life goal of botany. She did sewing for hire, took in individual boarders at first, and finally (1900–1910) established a boarding house to provide funds for Jones to continue his work. Jones had three main goals; to collect the flora of the West, to publish a treatment of *Astragalus*, and to write a flora of the Great

Fig. 7. George Engelmann (ca 1864), specialist in cacti, yucca, agave, and conifers, and correspondent of Parry, Jones, Siler, and others (photo courtesy of Richard W. Pohl).

Basin. All funds provided by Anna and by himself, from mining, consulting, writing, and other projects, were technically supposed to go toward accomplishing of these goals. But Jones was not good at managing money, expending large quantities of capital in photography and unwise investments. Anna lived to see practically all of the first goal and much of the second one completed. Jones had essentially completed the manuscript of *Astragalus* by 1910 (Barneby 1964). Neither Anna nor Marcus would live to see the final goal attained. The Great Basin flora would remain for others.

Broaddus (1952) notes of her mother that "The last year of her life whe spent in Claremont, California, keeping house for her youngest child, Mildred, to help her finish college, and earning what she could by doing dress making." Mildred was one of three children; the others were Howard and Mabel (Broaddus 1952).

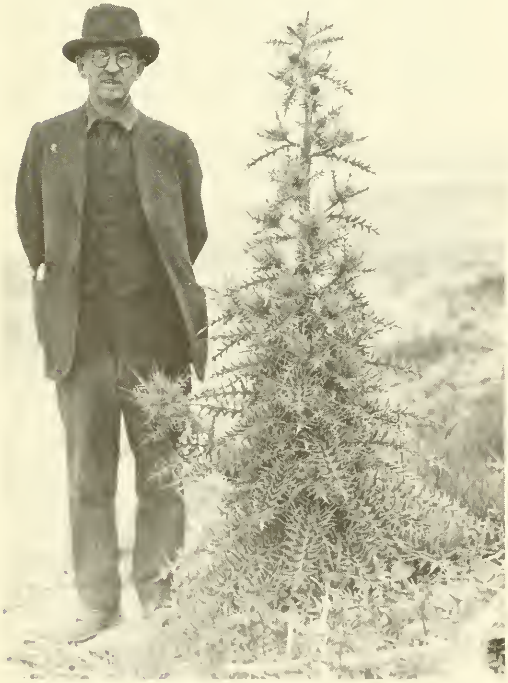


Fig. 8. Albert Osbun Garrett (ca 1930), resident Utah plant taxonomist for more than five decades, teacher, collector, and author of six editions of the *Spring Flora of the Wasatch* (photo courtesy of Lois Arnow).

It is not surprising that Jones was able to accomplish so much, with a wife so dedicated to his care and to his cause.

His trip to St. George required 22 days, but he returned to Salt Lake City in just 16 days. This compares with a drive of about seven hours each way today. The state must have seemed overwhelmingly large to Jones, as it still remains, but his youthful enthusiasm seems to have overshadowed any doubts regarding size or complexity of the flora.

In the ensuing decades he researched a surprising number of places, including many of the mining areas such as Frisco, Silver Reef, Detroit, and Eureka. The state, despite its great size, did not occupy all his time. He traveled to California, Nevada, Montana, Arizona, and finally to Mexico, but his preoccupation with Utah plants is evident from his accomplishments. During his 43 years as resident botanist for Utah this resourceful person built a personal herbarium of about 100,000 unmounted sheets (Munz 1965), among them the best set of Utah plants assembled in all history. Included among that herbarium were 305 Utah types, almost three-tenths of all types collected in the state between 1843 and 1981. Additionally, Jones had named some 165 plant taxa based on Utah types, mainly on his own collections.

If that was not enough, Jones, after becoming disgruntled with other publishers (his life is filled with examples of being disgruntled), began to print his own journal "Contributions to Western Botany," on a hand-operated press, using badly worn type, at his home on the avenues in Salt Lake City. This remarkable pioneer undertook to complete a revision of the genus *Astragalus* for North America. Difficult was the task, at any time, but Jones also faced the problems of transportation, communication, and paucity of library materials; and, though largely dependent on his own collections, his meager locality data is encyclopedic when compared to that recorded (or unrecorded) by some of his contemporaries.

Despite these hurdles, the revision of *Astragalus* was essentially completed by 1910 (Barneby 1964). It was not published until 1923, apparently printed as were his "Contributions" on his own press, with worn type. The text was distributed on "Feb. 15, 1923" and the plates on "June 20, 1923" (Jones 1923).

In that same year, Jones's herbarium was purchased by Miss Ellen B. Scripps of La Jolla, California for Pomona College, Claremont, California. That herbarium, the richest of any in Jones's first set of Utah type material, resides today at Rancho Santa Ana Botanical Garden, having been integrated therein in the 1960s.

The species concept of Jones was similar to that of Asa Gray, the leading 19th century botanist with whom Jones corresponded, and to whom he sent early sets of his western collections. A tribute to Jones abilities is indicated in the fact that more than half of the taxa named by him from Utah are still accorded taxonomic standing in contemporary treatments.

He came to look upon western American plant taxonomy as his own, and summarily defended his territory against all comers. His ego was monumental, but was occasionally tempored by flashes of knowledge that he might not be omnipotent. The field season of 1894 (Jones 1895) found him in the field, hired by the U.S. Department of Agriculture as "Special Field Agent." It was to be his best year, with "about 50,000 specimens and 1700 sets, there being 1106 species and varieties in the sets . . ." Or, (Munz 1965) "The total number collected was 4060, and about 35,000 specimens," depending on which of the two accounts of the season one is to believe. Jones (1895) opened the introductory remarks of the report of the 1894 collections, which is the most remarkable single publication in Utah's history of botanical exploration, with the following sentence: "Having had an opportunity to examine the material in the National Herbarium I have been able to correct many errors, and possibly to make a few more." That publication, Jones's "Contributions to Western Botany. No. VII.", reported on some 119 new taxa for Utah, inter alia. That record will stand for all time. The report was published in "Proceedings of the California Academy (Second Series, Vol. 5)," and was one of the last of his contributions published elsewhere (Jones 1895).

There was no one free from Jones's criticism, which resulted from a growing paranoia due in part to his isolation from the centers of botanical investigation in the country, and in part to the lack of recognition for his contributions, which are staggering. Nevertheless, his criticisms recounted herein were largely unfounded. His contemporaries were, with some exceptions, honorable men doing work in the best tradition open to them. They were, in their own ways, as isolated and as unrecognized as Jones. His published attacks on them yield information and insight into them and him. They are cited here for that reason. Jones thought of himself as benevolent and charitable.

The following examples are presented to give an idea of the time in which Jones lived, and to give a portion of the cast of characters who wandered through Jones's existence as a botanist.

In his "Contributions to Western Botany. No. 12" (1908), Jones took N. L. Britton to task for provisions of the American Association for Advancement of Science attempt at botancial nomenclature. One should know that no standardized code was acceptable to the botanists in the United States at that time, and one would not be forthcoming until publication of the International Code of Botanical Nomenclature in 1935, following Jones's death. Jones wrote of the Brittonian attempt: "Its chief virtue was in a rigid adherence to priority," and further ". . . we find that it isn't priority if it goes back farther than 1753, and it is not priority if it is not in the Latin language." And, still further; "If it is contended that common terms are not Latin we can easily follow the lead of Britton and put a Latin tail on them (a la *Manihota* Britton for Manihot). In that case we would have such very attractive combinations as the following: *Sagebrushum tridentatum*, *Brittonastrum tumbleweedum*, *Greenella slipperyelma*, *Rydbergionella bitterroota*, *Covillea creosotebusha*, *Nelsonella greasewooda*, etc."l

Jones did not agree with acceptance of 1753 as the starting date for botanical nomenclature, and neither did he believe that synonyms should stand in the way of a subsequent use of those same names. Latin as an official language for publication of new species was unacceptable. Jones (1908) wrote: "The purpose of science is to clarify, . . . so that those who follow us can take up work where we left off and ultimately bring out all the underlying facts and explain causes of natural phenomena." Latin, which was included in his formal education at Grinnell College, and which he had taught in the late 1870s, would not add to clarification for those who would follow him, he thought.

Jones carried his criticism to Dr. B. T. Butler who published a treatment of the western American birches in the Bulletin of the Torrey Botanical Club in August of 1909. After systematically chastising Butler on the merits of his work, which criticisms were merited, if not pleasantly couched, he unfairly attacked the education of Butler and the quality of his teachers (Jones 1910). "The writer [Jones] would be glad to subscribe several cents toward a fund for the education of the professors who are responsible for this kind of work so that they might go to some botanical kindergarten where they could learn that a plant growing in the shade or on a north slope or in a cold lake will differ from another from the same parent which grows in a warmer and drier situation, and that this condition will be reversed when the offspring of these plants occupy reversed conditions; and where they could learn that a poodle dog running around a house is not necessarily two distinct species because they see his tail only on the south side and later on his head only on the north side."

Perhaps, but not likely, Jones would have been less harsh on Dr. Butler, but that student took his Ph.D. degree at Bronx Park and Columbia, always synonymous to Jones with gross misunderstanding of "true" botany. Jones attacked members of the Brittonian school, especially P. A. Rydberg and those associated with him. An enlightening aside on the Brittonian school is found in Jones's (Jones 1913: 27) comments on Gray's Manual, Seventh Edition, in which he states; "One of the most commendable things in the book is the ignoring of the split genera of Britton, Rydberg, and Small. For some years the Brittonians have raised a great hue and cry about the new and original work done by them in splitting up Grayan genera. A recent repetition of this is in the Torrey Bulletin where the new Manual was reviewed through Bronx Park glasses. Anything published by Harvard is like a red flag before a bull to Bronx Park. Whenever Harvard sneezes Bronx Park has a fit, and it is a standing joke among botanists." Jones (1913) then discusses the work by Rydberg in *Habenaria*; "As though Rydberg had done any original work in the genus." And further, "Rydberg tries to justify this work by saying that some of the changes have already been recognized by Europaean botanists. Now if there is any crazy thing that some European botanist has not done in the near or remote past the writer would like to have it mentioned, and to use that as an excuse for doing some other crazy thing is no argument in its favor." The last sentence is as applicable today as it was when Jones wrote it. Some contemporary American botanists look to Europe as the wellspring of all that is important or believable in 20th-century taxonomy. If the Europeans subscribe to splitting then we should follow. The idea is as absurd today as it was in Jones's time; the Europeans have mainly looked at their flora too long, if we have not looked long enough.

Jones was not without humor in his criticisms. He (1910: 34–42) wrote a rebuttal to a publication by A. A. Heller dealing with nomenclature. Jones wrote: "The publication of the article on nomenclature in my last Contributions seems to have given Mr. Heller (in Muhlenbergia) a bad attack of mental colic, recurrent colic. His capacity to appreciate the motive and scope of my criticisms reminds one of the Englishman who after traveling extensively in this country returned home and said to his admiring friends 'The Americans are a very clever people but they have many uncouth expressions, for example they say 'Where am I at', we would say 'Where his my at.' ' "

Jones (1910: 35) continued his argument against the principal of priority begun earlier (Jones 1908). After giving other examples of treating names from languages other than Latin, he notes, "Now that he [Heller] has Hellerized all the English names . . . and gotten the Hellerian tail properly adjusted to all, he will find that Greek antedates the English, then can get up another set of names from the Sanscrit, then the Chinese, then he might take up the Egyptian and give still another batch of new names. By the time the botanical public has begun to reccover from the last of these afflictions it is likely that the phonograph and the graphophone will be perfected that they can take the ripple marks made by sound waves on prehistoric mud (now turned to stone) produced by the incoherent babblings of some of the simian ancestors of the Brittonians, and reproduce them so that they will be as lucid as some recent descriptions of plants, and will have far stronger claim to priority of publication than the Brittonian checklist had at the time when it was said to have been published."

Jones was wrong to oppose the principal of priority, and because of his obstinacy, he created synonyms that were unjustified, i.e., the case of *Astragalus angustus* (Jones) Jones, wherein he refused to use the legitimate replacement "*ceramicus*" proposed by Sheldon because earlier names were already occupied. Priority ultimately provides for a stability in nomenclature; without it chaos could result. Jones should have understood the necessity for a consistent nomenclature.

In the same article in which Jones (1910: 35) attacked Heller, he took the opportunity for a broadside against P. A. Rydberg and E. L. Greene. "Greene and Rydberg especially have been addicted to bolstering up fictitious species and genera by reasoning from analogy instead of known facts. Such arguments always get their users into difficulty. I well remember when it was a stock argument among geologists to claim that the climate of the Arctic was Tropical in the early Quaternary because elephants (mastodons) lived there, animals which live only in Tropical climates. Many years afterwards one of these animals was found in a perfect state of preservation imbedded in ice, and it proved to have very long hair and its stomach was full of Arctic plants which it had eaten, showing that it had its home in a frigid climate where that race of animals flourished, and not Tropical as has been dogmatically assumed," Jones wrote.

The mastodon case is cited by Creationists in contemporary literature as demonstrating existence of tropical climates in high latitudes, but the plants taken from frozen stomach contents are said to consist of tropical plants., i.e., buttercups for example. The rattle-headed thinking alluded to by Jones, if not altogether warranted in the men he attacked, is not attributable to botanists alone.

Barneby (1964) has indicated that Jones was wrong in his malicious attacks, especially of Rydberg. There is logic in Rydberg's approach, even if that approach is subject to interpretation. He believed in the binomial system of nomenclature strictly. He (Rydberg 1929) believed that the variation which he observed, and he was a keen observer, should be described. Such an approach called to attention those who were his contemporaries and those who followed him. His work was always limited to those few specimens he had available. That he should see only portions of the entire picture is a fault not his alone; all botanists are troubled with the same problem in varying degree.

But, it was on Greene and Rydberg that Jones showered his continuing invective. He survived both of them, and heaped indignation on them in their later years, and in Greene's case, even following his death.

E. L. Greene died on 10 November 1915. Presumeably Jones wrote his scathing obituary of Greene shortly thereafter, but it was

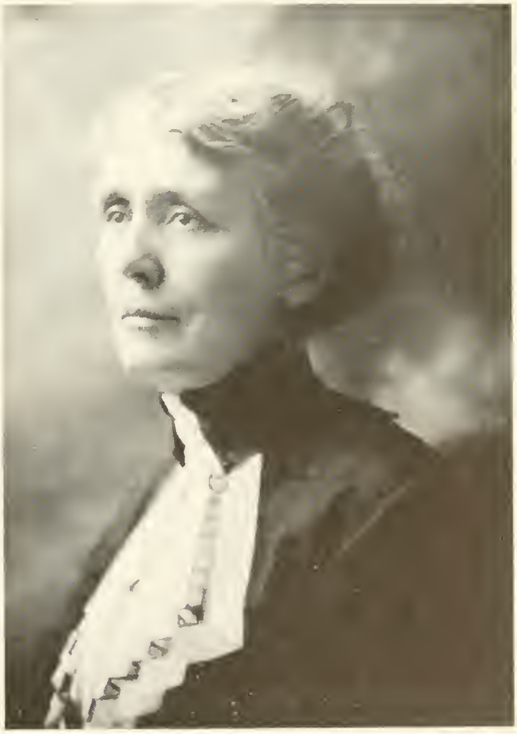


Fig. 9. Anna Elizabeth Richardson Jones (1913), wife of Marcus Eugene Jones, who helped him to collect, and who provided money to support him in his botanical works (photo courtesy of Charles Walker).

not published until a decade and a half later (Jones 1929). The opening paragraph of the paper (Jones 1929: 25) entitled "Greene" is as follows. "There have been several notable deaths in the botanical world since my last contributions. Greene, the pest of systematic botany, has gone and relieved us from his botanical drivel. They say that the good that men do lives after them, but the evil is enterred with their bones. I suspect that his grave must have been a big one to hold it all." Subsequently, Jones (1929) continues; "Greene was first, last and all the time a botanical crook, and an unmitigated liar, when it suited him to try to make a point against someone else."

Rydberg survived until July of 1931, and had published his monumental Flora of the Rocky Mountains first in 1917. The work was reissued in revised form in 1922 (Rydberg 1917, 1922). Not until much later did Jones (1929: 9) take note of Rydberg's flora in print. The opening paragraph of Jones's review begins: "We are glad that at last Rydberg has put his conception of species and genera in book form. His sporadic publications hitherto have shown botanists that he has no conception of either species or genera. In addition he accommodates us by saying that any plant deserving of a name should have a specific name. What he really means is that if any fool botanist anywhere in the world has applied a name to a plant as variety form or subspecies that name should be raised at once to specific rank, and which he proceeds to do. At the same time he quibbles over priority by position as though it was a matter of any importance. He 'strains at a gnat and swallows a camel.' "

"This book is what I have in the past dubbed bughole botany, species depending on the number of bugholes in the leaves. Rydberg has no conception that there is any such science as ecology, or that environment has any effect on species variation."

Jones (1935, published posthumously) wrote an obituary for Rydberg also, in which he was more a gentleman, but the rancor comes through even then. Jones, it seems, never knew when to let an argument end, even when there was no chance for his opponent to speak. Jones (1935: 141) states: "On July 25, 1931 there occurred the second tragedy in American botany, the death of Rydberg before his time, the first tragedy having been the death of J. N. Rose. Their disappointment at the treatment accorded them by the botanical public was, however, partly their own fault; for no one has a right to subordinate his own judgment to that of another, as I think they did to Britton's, for the sake of financial support." Later, Jones (1935: 142) continued, "Rydberg was inclined in his later years to consider himself persecuted. I never knew that he had any personal enemies. Nor do I think any one ever got after him for personal reasons. I certainly never did, though once or twice I had some reason to feel that he had not treated me fairly in private correspondence."

Ivar Tidestrom and Aven Nelson were subjects of his invective too, and not without some justification. They were troubled by a lack of material to make definitive taxonomic decisions, and they lacked the experience and understanding that Jones had accumulated in his decades of active field and herbarium studies. Despite the quality of their work, as is apparent in their publications (Tidestrom 1925, Coulter & Nelson 1909), their floras were to stand for decades as the authorities on plant names for much of the Rocky Mountain and intermountain regions. The publications were used by generations of botanists who were never quite satisfied with keys, descriptions (lacking altogether in the work by Tidestrom), or geographical data. The shame in all of Jones's criticism is that he did not complete a work on the flora of the Basin and Range Province of his own. It, too, would have been flawed, as all works are, but with evidence taken over a long lifetime (more than four decades), it would have served well those later generations on whom was afflicted the work of Tidestrom, and the peripheral work of Coulter & Nelson. Jones's opus magnus laboris, his revision of *Astragalus* (1923) is flawed, not by the species concept or by the descriptions, but by the rattleheaded polychotomous keys, which are difficult if not impossible to follow, and by his persistence in following his own code of nomenclature. The keys, of which he felt unjustifiably proud (as noted by Barneby 1964), are based on a complex number and letter sequence, which leaves the user wondering where one goes from any particular place. That his species concept has stood the test of time is indicated again in the work by Barneby (1964), who published a revision of the North American species of *Astragalus* some four decades following the appearance of Jones (1923) work on that incredible genus. Barneby was able to recognize some 60 percent of the taxa named in that genus by Jones, but only 38 percent of those named by Rydberg, and most of those at varietal rank.

Jones had "seen more of the elephant," as it were, than his contemporaries, and with his abilities of observation and his acute awareness of more of it than any other of the period, it is presumed that he would have described both trunk and tail properly and have known their approximate locations. His contemporaries suffered, as do many of our own generation of taxonomists, with a myopia of understanding, and they are caught up in preconceived notions of the importance of plant characteristics.

Rydberg let the characteristics of pods in *Astragalus*, which he likewise monographed (1929), dictate its segregation into more than 30 genera. Carried to its logical conclusion, pod features would ultimately trap its user into absurdities. The use of pod types led Rydberg to place plants of almost identical vegetative appearance into separate genera (i.e., *Astragalus oophorus* Wats. var. *caulescens* (Jones) Jones in the genus *Phaca* and *Astragalus beckwethii* T. & G. in the genus *Phacomene*). Uniformity in plant taxonomy is a trap laid by taxonomists, because the plants vary in accordance with dictates of genotype as that is influenced by habitat. Too, each taxonomic unit is the result of the genetic pathways that produced it, and each is unique both in pathway and in end result. The system must be made to fit the plants, not the other way around. Still, we allow ourselves to fall into the rut; perhaps we demand that we do.

In a presentation to the Fourth International Botanical Congress Rydberg (1929a) outlined his approach to naming of plants. The paper is entitled "Scylla or Charybdis," in recognition of the pitfalls of the descriptive taxonomist. Rydberg (1929a: 1539) notes, "I will admit that phytographic work in the last 35 years has been overdone and I myself can scarcely plead 'not guilty' to such a charge." A portion of the problem of "over description" was recognized as duplication of effort, where one taxonomist did not know that the entity was already described. "...the more the taxonomist studies a genus or a family, the more forms he recognizes, and the better he knows the family, the finer splitter he becomes. Then he either distinguishes more restricted genera, or recognizes infinitesimal species; or perhaps he recognizes large genera and broad species, but splits these into numerous subordinate categories: subgenera, sections, groups, subspecies, varieties, forms, etc., without end." Thus, Rydberg outlined the directions which he recognized at the ends of the spectrum of taxonomic studies.

His case was overstated, because not all taxonomists are polarized to either one of the two extremes. Rather, they fall remarkably between, because most taxonomists let reality, as they understand it, dictate the course they should follow. It is true that reality is subject to interpretation, and no one can admit to understanding all of what is real. But few ignore the information that is available

Fig. 10. Marcus Eugene Jones (1891), with his field equipment and plant press, south of Salt Lake City (photo Courtesy of Charles Walker).

to them; their interpretations approach reality, more or less.

The thesis of Rydberg's speech (1929) revolves around the publication of the "Phylogenetic Method in Taxonomy" (Hall and Clements 1923). He (Rydberg 1929: 1540) states, "We have seen the endless and infinitesimal splitting into categories of the German school and for twenty years have been thoroughly disgusted with their absurd nomenclature of trinomials, quadrinomials, and polynomials. We believed that any form that is worth describing is worth a name and that a binomial is better than any other. But we might have forgotten that there is a Scylla as well as a Charybdis."

The defence of Rydberg would have been easier except for his "leaping over the edge" in the direction of recognizing all variants at species level. For the feeling expressed in his paper that he had created the species, and had defended and upheld the creations of others, he states, "For years I have admitted that I am a splitter, but I have prided myself on being consistent, as, for instance, in splitting some genera so as to make them equivalent to other genera in the same family or tribe, but I have just discovered that in order to save already described species of other botanists, even if they have a meager excuse for their existence, I have added some of my own of the same category and made my species concept very inconsistent."

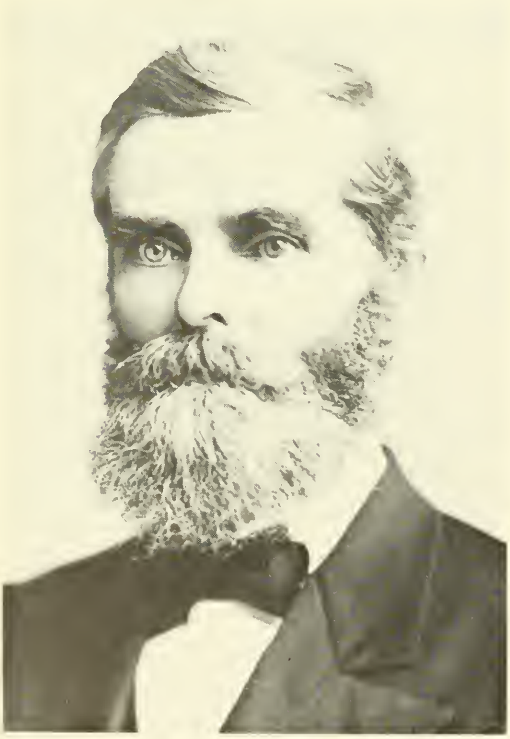


Fig. 11. Charles Christopher Parry (ca 1870), student of John Torrey, correspondent of Asa Gray, Sereno Watson, and George Engelmann, and important collector of Utah types in 1874 (photo courtesy of Richard W. Pohl).

Despite the frailties of his approach, Rydberg was a gentleman. He did not attack Jones in the press, as Jones attacked him. Time will serve to judge them both.

Edward L. Greene (Ewan 1950) was attacked more heartily than any of Jones's other contemporaries, and with more justification. Of the 44 taxa named by him from within Utah only 3 stand in modern taxonomic treatments. He did not collect from within the state, and relied on plants taken by others for the basis of his taxonomic decisions. Perhaps Jones would have been less harsh in criticism of Greene if he had chosen more substantial variants for naming. But Greene was the product of his background, as was Jones, and that background involved training in the clergy (he was a minister). He seems to have believed in the concept of fixity of species, and that any variant was therefore worthy of a name. He also considered himself to be a linguist and would change names involving compounds of Latin and Greek together, without even knowing about the plants themselves. Time has served to judge him, at least as far as his Utah plant names are concerned, as incompetent. Jones judged him more harshly than that.

The career of Marcus Eugene Jones ended suddenly, as noted by his daughter, Mabel Jones Broaddus. In Contributions to Western Botany. No. 18. (1935: 132) she wrote: "At this point on June 3, 1934, my father, Prof. Marcus E. Jones met with a fatal accident. He was returning alone from a day's field trip in the San Bernadino Mts. enjoyed in company with the Samuel B. Parish Botanical Society when, at an intersection in San Bernadino, his car was struck in the rear by another car and overturned."

Marcus Jones (Jones and Broaddus 1952) was ". . . a man of unusual ability, strong character, and amazing versatility. . . . his central interest was always botany."

Jones's contributions to the understanding of Utah plant taxonomy are overwhelming. He cannot be equaled or surpassed.

Utah Plant Types

Abies subalpina Engelm. ex Ward Amer. Naturalist 10: 555. 1876. Pinaceae. = *A. lasiocarpa* (Hook.) Nutt. Sanpete (?) Co., Wasatch Pl., above Gunnison, Ward sn, 1875 (US!).

Abronia argillosa Welsh & Goodrich Great Basin Naturalist 40: 78. 1980. Nyctaginaceae. Grand Co., 6 mi s Cisco, S, E., & M. Welsh 16689, 1978 (BRY!;NY!; US!;UT!).

Abronia fallax **Heimerl ex Rydb.** Bull. Torrey Bot. Club 29: 684. 1902. Nyctaginaceae. = *A. elliptica* A. Nels. Salt Lake Co., Salt Lake City, Jones 1337, 1879 (US!;NY!;UTC!).

Abronia fragrans **Nutt. ex Hook. var.** ***pterocarpa*** Jones Contr. W. Bot. 11: 3. 1903. Nyctaginaceae. = *A. elliptica* A. Nels. Tooele Co., Cottonwood, near Johnson Pass, Jones sn, 1900 (?).

Abronia micrantha **Torr. var.** ***pedunculata*** Jones. Proc. Calif. Acad. II. 5: 716. 1895. Nyctaginaceae. = *Tripterocalyx micrantha* (Torr.) Hook. Washington Co., St. George, Jones 5101, 1894 (POM!;US!;BRY!;RM!).

Abronia nana Wats. Proc. Amer. Acad. 14: 294. 1879. Nyctaginaceae. Beaver Co., near Beaver City, Palmer 404 12, 1877 (ISC!).

Abronia pumila Rydb. Bull. Torrey Bot. Club 29: 683. 1902. Nyctaginaceae. = *A. elliptica* A. Nels. Emery Co., Emery, Jones 5545q, 1894 (US!;POM!;NY!).

Abronia salsa Rydb. Bull. Torrey Bot. Club 29: 684. 1902. Nyctaginaceae. = *A. elliptica* A. Nels. Salt Lake Co., Salt Lake City, Watson 965, 1869 (NY!;US!).

Abronia turbinata **var.** ***marginata*** Eastw. Proc. Calif. Acad. II, 6: 313. 1896. Nyctaginaceae. = *A. fragrans* Nutt. San Juan Co., Bartons range, Eastwood sn, 1895 (CAS!).

Acerates decumbens **var.** ***erecta*** Durand Trans. Amer. Phil. Soc. 11: 174. 1860. Asclepiadaceae. = *Asclepias asperula* (Decne.) Woodson Salt Lake Co., Salt Lake City, Carrington sn, 1857 (P).

Acer kingii **Britt. in Britt. & Shafer** N. Amer. Trees 656. 1908. Aceraceae. = *A. negundo* var. *interius* (Britt.) Sarg. Wasatch Mts., Watson 216, 1869 (US!).

Acer sacharum **Marsh. var.** ***trilobum*** **E. Murray** Kalmia 10: 2. 1980. Aceraceae. = *A. grandidentatum* Nutt. Sanpete Co., Ephraim Canyon, Tidestrom 1003, 1908 (US!).

Aconitum divaricatum **Rydb.** Fl. Rocky Mts. 314, 1062. 1917. Ranunculaceae. = *A. columbianum* Nutt. in T. & G. Salt Lake Co., City Creek Canyon, Leonard 204182, 1884 (NY!).

Aconitum glaberrimum Rydb. Bull. Torrey Bot. Club 29: 151. 1902. Ranunculaceae. = *A. columbianum* Nutt. in T. & G. Washington (?) Co., (S. Utah) Palmer 11, 1877 (NY!).

Actinella biennis Gray Proc. Amer. Acad. 13: 373. 1878. Asteraceae. = *Hymenoxys cooperi* (Gray) Cockerell Washington (?) Co., Arizona and Utah, Palmer 260, 1877 (US!;ISC!;BRY!).

Adiantum rimicola Slosson Bull. Torrey Bot. Club 41: 308. 1914. Polypodiaceae. = *A. capillus-veneris* var. *modestum* f. *rimicola* (Slosson) Fern. San Juan Co, Armstrong Canyon, Rydberg & Garrett 9423, 1913 (NY!).

Agave scaphoidea **Greenm. & Roush** Ann. Missouri Bot. Gard. 16: 391. 1929. Agavaceae. = *A. utahensis* Engelm. var. *utahensis* Washington Co., St. George, Palmer sn, 1877 (MO?).

Agave utahensis **Engelm. in Wats. var.** ***utahensis*** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 497. 1871. Agavaceae. Washington Co., St. George, Palmer s.n. 1870 (US!).

Agoseris caudata **Greene** Leafl. Bot. Obs. & Crit. 2: 124. 1911. Asteraceae. = *A. glauca* (Pursh) Raf. var. *laciniata* (D.C. Eaton) Smiley Sevier Co., Salina Canyon, Jones 5438, 1894 (US!;NY!).

Agoseris confinis **Greene** Leafl. Bot. Obs. & Crit. 2: 124. 1911. Asteraceae. = *A. aurantiaca* (Hook.) Greene Piute Co., near Marysvale, Jones 5893z, 1894 (US!).

Agoseris isomeris **Greene** Leafl. Bot. Obs. & Crit. 2: 123. 1911. Asteraceae. = *A. glauca* (Pursh) Raf. Summit Co., Uinta Mts., Goodding 1397, 1902 (US!;RM!;ISC!).

Agoseris longirostris **Greene** Leafl. Bot. Obs. & Crit. 2: 125. 1911. Asteraceae. = *A. aurantiaca* (Hook.) Greene Sevier Co., Fish Lake, Jones 5743N, 1894 (US!;POM!).

Agoseris taraxacoides **Greene** Leafl. Bot. Obs. & Crit. 2: 123. 1911. Asteraceae. = *A. glauca* (Pursh) Raf. Piute Co., near Marysvale, Jones 5372, 1894 (US!).

Aletes tenuifolia **Coult. & Rose** Contr. U.S. Natl. Herb. 7: 108. 1900. Apiaceae. = *Musineon lineare* (Rydb.) Mathias Cache Co., Rydberg sn, 1895 (US!;RM!;NY!).

Allium biceptrum **var.** ***utahense*** **Jones** Contr. W. Bot. 10: 33. 1902. Liliaceae. = *A. biceptrum* var. *biceptrum* Salt Lake Co., City Creek Canyon, Jones 6647, 1898 (POM!).

Allium brevistylum Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 350. 1871. Liliaceae. Summit Co., Uinta Mts., Watson 1180, 1869 (US!;NY!).

Allium cristatum Wats. Proc. Amer. Acad. 14: 232. 1879. Liliaceae. = *A. nevadense* Wats. Washington Co., St. George, Palmer 454, 1877 (US!;NY!;ISC!).

Allium passeyi **A. & N. Holmgren** Brittonia 26: 309. 1974. Liliaceae. Box Elder Co., Howell Valley, Holmgren et al. 13125, 1960 (NY!;BRY!;US!;UT!;UTC!).

Allium reticulatum **var.** ***deserticola*** **Jones** Contr. W. Bot. 10: 30. 1902. Liliaceae. = *A. macropetalum* Rydb. Grand Co., Cisco, Jones sn, 1890 (POM!;US!).

Allium tribracteatum **Torr. var.** ***diehlii*** **Jones** Contr. W. Bot. 10: 18. 1902. Liliaceae. = *A. brandegei* Wats. Summit Co., Parleys Park, Jones 6590, 1901 (US!;CAS!POM!).

Allocarya cognata Greene Pittonia 4: 235. 1901. Boraginaceae. = *Plagiobothrys scouleri* (H. & A.) Johnst. Cache Co., Cache Valley, Mulford sn, 1888 (US!;NDG!).

Allocarya orthocarpa Greene Pittonia 3: 109. 1896. Boraginaceae. = *Plagiobothrys leptocladus* (Greene) Johnst. Cache Co., Mulford sn, 1898 (US!;NDG!).

Alsine palmeri Rydb. Bull. Torrey Bot. Club 39: 315. 1912. Caryophyllaceae. = *Stellaria obtusa* Engelm. Beaver Co., Beaver Valley, Palmer 54, 1877 (NY!).

Amelanchier utahensis Koehne Wiss. Bei. Progr. Falk- Realgym. Berl. 95: 25. 1890. Rosaceae. Washington Co., Belleview, Jones 1716, 1880 (US!;POM!;UTC!).

Amelanchier utahensis Koehne var. _cinerea_ Goodding Bot. Gaz. 37: 55. 1904. Rosaceae. Washington Co., St. George, Goodding 780, 1902 (RM!).

Amsinckia eatonii Suksd. Werdenda 1: 64. 1931. Boraginaceae. = *A. retrorsa* Suksd. Utah, Eaton 251, 1869 (CAS!).

Amsinckia utahensis Suksd. Werdenda 1: 106. 1931. Boraginaceae. = *A. tessellata* Gray Salt Lake Co., Salt Lake City, Vicker sn, 1901 (UC!).

Amsonia brevifolia Gray Proc. Amer. Acad. 12: 64. 1876. Apocynaceae. = *A. jonesii* Woodson Washington (?) Co., Palmer 302, 1877 (NY!).

Amsonia eastwoodiana Rydb. Bull. Torrey Bot. Club 40: 465. 1913. Apocynaceae. Grand Co., Moab vicinity, Rydberg & Garrett 8468, 1911 (NY!;RM!;US!).

Amsonia latifolia Jones Contr. W. Bot. 12: 50. 1908. Apocynaceae. = *A. jonesii* Woodson Sevier Co., Monroe Jones 6446, 1899 (CAS!;US!;RM!;POM!;BRY!;NY!).

Androstephium breviflorum Wats. Amer. Naturalist 7: 303. 1873. Liliaceae. Syn: *Brodiaea paysonii* A. Nels. Kane Co., near Kanab, Thompson 59, 1872 (US!).

Anemone stylosa A. Nels. Bot. Gaz. 42: 52. 1906. Ranunculaceae. = *A. multifida* Poir. Sevier Co., Fish Lake, Jones 5763, 1894 (US!;BRY!;RM!;POM!;NY!).

Angelica dilatata A. Nels. in Coult. & Rose Contr. U.S. Natl. Herb. 12: 446. 1909. Apiaceae. = *A. wheeleri* Wats. Salt Lake Co., City Creek Canyon, Garrett 2127, 1907 (US!;RM!).

Angelica leporina Wats. Proc. Amer. Acad. 12: 252. 1871. Apiaceae. = *A. pinnata* Wats. Wayne Co., Rabbit Valley, Ward 612, 1875 (US!;NY!).

Angelica pinnata Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 126. 1871. Apiaceae. Syn: *A. leporina Wats.* Summit Co., Uinta Mts. Watson 458, 1869 (US!;NY!).

Angelica wheeleri Wats. Amer. Naturalist 7: 301. 1873. Apiaceae. Syn: *A. dilatata* A. Nels. Northern and Central Utah, Wheeler 1872 (US!).

Anotites jonesii Greene Leafl. Bot. Obs. & Crit. 1: 102. 1905. Caryophyllaceae. = *Silene menziesii* Hook. Utah Co., American Fork Canyon, Jones 1372, 1880 (US!;RM!;POM!;UTC!).

Antennaria austromontana E. Nels. Proc. U.S. Natl. Mus. 23: 703. 1901. Asteraceae. = *A. alpina* var. *media* (Greene) Jeps. Piute Co., Marysvale, Jones 5522, 1894 (US!).

Antennaria dimorpha (Nutt.) T. & G. var. _macrocephala_ D.C. Eaton Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 186. 1871. Asteraceae. = *A. dimorpha* (Nutt.) T. & G. Salt Lake Co., Salt Lake City, Watson 654, 1869 (US!).

Antennaria obtusata Greene Feddes Repert. 5: 241. 1908. Asteraceae. = *A. parvifolia* Nutt. Uintah Co., Uinta Mts., Goodding 1209, 1902 (US!).

Anticlea vaginata Rydb. Bull. Torrey Bot. Club 39: 108. 1912. Liliaceae. = *Zigadenus vaginatus* (Rydb.) Macbr. San Juan Co., Natural Bridges, Rydberg & Garrett 9407, 1911 (NY!;RM!;US!;BRY!;UT!).

Antirrhinum kingii Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 215. 1871. Scrophulariaceae. Tooele Co., Stansbury Island, Watson 767, 1869 (US!).

Aquilegia caerulea James var. _calcarea_ Jones Proc. Calif. Acad. II 5: 619. 1895. Ranunculaceae. = *A. scopulorum* var. *calcarea* (Jones) Munz Garfield Co., above Cannonville, Jones 5312a, 1894 (POM!;US!).

Aquilegia depauperata Jones Contr. W. Bot. 8: 1. 1898. Ranunculaceae. = *A. flavescens* Wats. Utah Co., Provo Canyon, Jones sn, 1896 (POM!;US!).

Aquilegia flavescens Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 10. 1871. Ranunculaceae. Syn: *A. depauperata* Jones Salt Lake (?) Co., Wasatch Mts., Watson 35, 1869 (US!;NY!).

Aquilegia flavescens Wats. f. _minor_ Tidestr. Amer. Midl. Naturalist 1: 171. 1910. Ranunculaceae. Sanpete Co., Wasatch Plateau, Tidestrom sn (?).

Aquilegia micrantha Eastw. Proc. Calif. Acad. II, 4: 559. 1895. Ranunculaceae. Syn: *A. pallens* Payson; *A. lithophila* Payson; *A. rubicunda* Tidestr. San Juan Co., near Bluff City, Wetherill sn, 1894 (CAS!;POM!).

Aquilegia pallens Payson Bot. Gaz. 60: 375. 1915. Ranunculaceae. = *A. micrantha* Eastw. San Juan Co., LaSal Creek, Payson 443, 1914 (?).

Aquilegia rubicunda Tidestr. Amer. Midl. Naturalist 1: 168. 1910. Ranunculaceae. = *A. micrantha* Eastw. Emery Co., near Emery, Tidestrom 1418, 1908 (US!).

Aquilegia scopulorum Tidestr. Amer. Midl. Naturalist 1: 167. 1910. Ranunculaceae. Sanpete Co., Wasatch Peak, Tidestrom 1788, 1908 (US!).

Arabis demissa Greene var. _russeola_ Rollins Rhodora 43: 387. 1941. Brassicaceae. Uintah Co., 18 mi N Vernal, Rollins 1757, 1937 (NY!;US!;CAS!;RM!;BRY!;UTC!).

Arabis diehlii Jones Contr. W. Bot. 14: 38. 1912. Brassicaceae. = *A. pendulina* Greene Beaver Co., Mt. Belknap, Jones sn, 1899 (POM!).

Arabis glabra (L.) Bernh. var. _furcatipilis_ Hopkins Rhodora 39: 109. 1937. Brassicaceae. Cache Co., Logan Canyon, Maguire 3437, 1932 (RM!;UTC!).

Arabis hirsuta (L.) Scop. var. _laevis_ Tuzon Bericht Frein Verein Pflanzengeog. Syst. Bot. 1919: 43. 1921. Brassicaceae. = *A. hirsuta* (L.) Scop. Utah Co., American Fork Canyon, Jones sn, 1880 (UTC!).

Arabis lasiocarpa Rollins Systematic Botany 6: 58. 1981. Brassicaceae. Rich Co., 6 mi w Garden City, R.C. & K.W. Rollins 79307, 1979. (GH).

Arabis longirostris Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 73. 1871. Brassicaceae. = *Streptanthella longirostris* (Wats.) Rydb. Tooele Co., Stansbury Island, Watson 72, 1869 (NY!).

Arabis oreophila Rydb. Bull. Torrey Bot. Club 34: 437. 1907. Brassicaceae. = *A. lyallii* Wats. Salt Lake Co., Rydberg & Carlton 6678, 1905 (NY!).

Arabis pulchra Jones var. _duchesnensis_ Rollins Systematic Botany 6: 59. 1981. Brassicaceae. Duchesne Co., 3.8 mie Duchesne, R.C & K.W. Rollins 79113, 1979 (GH).

Arabis pulchra Jones var. _pallens_ Jones Contr. W. Bot. 14: 42. 1912. Brassicaceae. Grand Co., Westwater, Jones sn, 1891 (US!;NY!).

Arabis setulosa Greene Leafl. Bot. Obs. & Crit. 2: 81. 1910. Brassicaceae. = *A. pendulina* Greene Piute Co., Marysvale, Jones 5330, 1894 (US!;CAS!;POM!;NY!).

***Arabis stokesiae* Rydb.** Fl. Rocky Mts. 361, 1062. 1917. Brassicaceae. Syn: *A. divaricarpa* A. Nels.; = *A. confinis* Wats. Salt Lake Co., Parleys Canyon, Stokes sn, 1901 (US!;NY!).

***Aragallus majusculus* Greene** Proc. Biol. Soc. Wash. 18: 12. 1905. Fabaceae. = *Oxytropis sericea* Nutt. Garfield Co., Henry Mts., Jones 5674, 1894 (US!;POM!;NY!).

***Arctomecon humilis* Cov.** Proc. Biol. Soc. Washington 7: 67. 1892. Papaveraceae. Washington Co., St. George, Parry sn, 1874 (US!;NY!;ISC!;NDG!).

***Arenaria fendleri* (Rydb.) Fern. ssp. *brevifolia* Maguire** Madroño 6: 23. 1941. Caryophyllaceae. = *A. fendleri* var. *brevifolia* (Maguire) Maguire Grand Co., LaSal Mts., Maguire 17972, 1933 (UTC!).

***Arenaria filiorum* Maguire** Bull. Torrey Bot. Club 73: 326. 1946. Caryophyllaceae. Iron Co., beach, Navajo Lake, Maguire 19472, 1940 (NY!;BRY!).

***Arenaria hookeri* Nutt. in T. & G. var. *desertorum* Maguire** Amer. Midl. Naturalist 46: 506. 1951. Caryophyllaceae. Duchesne Co, near Duchesne, Ripley & Barneby 8701, 1947 (US!;NY!).

***Arenaria kingii* (Wats.) Jones ssp. *plateauensis* Maguire** Bull. Torrey Bot. Club 74: 54. 1947. Caryophyllaceae. = *A. kingii var. plateauensis* (Maguire) Reveal Iron Co., Cedar Breaks rim, Maguire 19024, 1940 (US!;NY!;UTC!).

***Arenaria nuttallii* Pax var. *gracilipes* Jones** Proc. Calif. Acad. II, 5: 626. 1895. Caryophyllaceae. = *A. nuttallii* Pax Piute Co., Brigham Peak, Jones 5951, 1894 (US!).

***Argemone corymbosa* Greene ssp. *arenicola* G. B. Ownbey** Mem. Torrey Bot. Club 21(1): 118. 1958. Papaveraceae. Emery Co., 37.9 mi sw Green River, Ownbey 2146, 1954 (US!;CAS!;RM!;BRY!).

***Arnica arachnoidea* Rydb.** N. Amer. Fl. 34: 353. 1927. Asteraceae. = *A. mollis* Hook. Salt Lake Co., Big Cottonwood Canyon, Rydberg & Carlton 6609, 1905 (NY!).

***Arnica caudata* Rydb.** Bull. Torrey Bot. Club 37: 463. 1910. Asteraceae. = *A. mollis* Hook. Salt Lake Co., Big Cottonwood Canyon, Garrett 1547, 1894 (RM!;NY!).

***Arnica chamissonis* Less. var. *longinodosa* A. Nels.** Bot. Gaz. 30: 199. 1900. Asteraceae. = *A. mollis* Hook. Piute Co., Marysvale, Jones 5883, 1894 (RM!;NY!).

***Arnica jonesii* Rydb.** Fl. Rocky Mts. 979. 1917. Asteraceae. = *A. latifolia* Bong. Salt Lake Co., Alta, Jones 119, 1879 (NY!;POM!;UTC!;NDG!).

***Arnica longifolia* D.C. Eaton in Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 186. 1871. Asteraceae. Summit Co., Uinta Mts., Watson 655, 1869 (NY!).

***Arnica ovata* Greene** Pittonia 4: 161. 1900. Asteraceae. = *A. mollis* Hook. Salt Lake Co., Alta, Jones 1128, 1879 (POM!;NY!;BRY!;UTC!;NDG!).

***Artemisia norvegica* Fries var. *piceetorum* Welsh & Goodrich in Welsh** Brittonia 33: 295. 1981. Asteraceae. Duchesne Co., Garfield Basin, Welsh et al 18970, 1979 (BRY!;NY!).

***Asclepias involucrata* Engelm. var. *tomentosa* Eastw.** Zoe 4: 120. 1893. Asclepiadaceae. = *A. macrosperma* Eastw. Grand Co., Courthouse Wash, Eastwood sn, 1892 (CAS!;NY!).

***Asclepias labriformis* Jones** Proc. Calif. Acad. II, 5: 708. 1895. Asclepiadaceae. Wayne Co., Capitol Wash, Jones 5650, 1894 (POM!;US!;RM!;BRY!;NY!).

***Asclepias leucophylla* Engelm. in Parry** Amer. Naturalist 9: 348. 1875. Asclepiadaceae. = *A. erosa* Torr. Washington Co., near St. George, Parry 207, 1874 (MO).

***Asclepias ruthiae* Maguire & Woodson** Ann. Missouri Bot. Gard. 28: 245. 1941. Asclepiadaceae. Emery Co., Calf Spring Canyon, Maguire 18310, 1940 (US!;UTC!).

***Asclepias welshii* N. & P. Holmgren** Brittonia 31: 110. 1979. Asclepiadaceae. Kane Co., Coral Pink Sand Dunes, N. & P. Holmgren 9009, 1978 (NY!;BRY!;UTC!).

***Astephanus utahensis* Englem. in Parry** Amer. Naturalist 9: 349. 1875. Asclepiadaceae. = *Cynanchum utahense* (Engelm.) Woodson Washington Co., near St. George, Parry 209, 1874 (ISC!).

***Aster canescens* Pursh var. *aristatus* Eastw.** Proc. Calif. Acad. II. 6: 296. 1896. Asteraceae. = *Machaeranthera canescens* (Pursh) Gray San Juan Co., Willow Creek, Eastwood 45, 1895 (CAS!).

***Aster glaucodes* Blake ssp. *pulcher* Blake** Proc. Biol. Soc. Washington 35: 174. 1922. Asteraceae. = *A. glaucodes* Blake var. *pulcher* (Blake) Kearney & Peebles Kane Co., Elk Ranch, Jones 6037, 1894 (US!;RM!;POM!).

***Aster glaucus* var. *wasatchensis* Jones** Proc. Calif. Acad. II. 5: 694. 1895. Asteraceae. = *A. wasatchensis* (Jones Blake Piute Co., near Marysvale, Jones 5861, 1894 (US!;RM!;BRY!;POM!;NY!).

***Aster halophilus* Greene** Leafl. Bot. Obs. & Crit. 2: 8. 1909. Asteraceae. = *A. chilensis* ssp. *adscendens* (Lindl.) Cronq. Salt Lake Co., Beck's Hot Springs, Garrett 2057, 1906 (UT!;NdDG!).

***Aster kingii* D.C. Eaton in Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 141. 1871. Asteraceae. = *Machaeranthera kingii* (D.C. Eaton) Cronq. & Keck. Salt Lake Co., Cottonwood Canyon, Watson 507, 1869 (US!;NY!).

***Aster leucopsis* Greene** Leafl. Bot. Obs. & Crit. 2: 8. 1909. Asteraceae. = *A. chilensis* ssp. *adscendens* (Lindl.) Cronq. Salt Lake Co., Salt Lake City, Garrett 1694, 1905 (UT!;NDG!).

***Aster thermalis* Jones** Proc. Calif. Acad. II, 5: 694. 1895. Asteraceae. = *A. pauciflorus* Nutt. Sevier Co., Monroe, Jones 5410, 1894 (POM!;US!).

***Aster venustus* Jones** Zoe 2: 247. 1891. Asteraceae. = *Machaeranthera venusta* (Jones) Cronq. & Keck. Grand Co., Cisco, Jones sn, 1890 (POM!;US!;CAS!;RM!;BRY!;NY!).

***Astragalus amphioxys* Gray var. *cymbellus* Jones** Rev. Astragalus 215. 1923. Fabaceae. = *A. cymboides* Jones Emery Co., San Rafael Swell, Jones sn, 1914 (POM!).

***Astragalus ampullarius* Wats.** Amer. Naturalist 7: 300. 1873. Fabaceae. Kane Co., Kanab, Thompson sn, 1872 (GH;US!).

***Astragalus araneosus* Sheld.** Bull. Geol. & Nat. Hist. Surv. Minnesota 9: 170. 1894. Fabaceae. = *A. lentiginosus* Dougl. var. *araneosus* (Sheld.) Barneby Beaver Co., Frisco, Jones 1807, 1880 (US!;RM!;BRY!;POM!;NY!;UT!;UTC!).

***Astragalus argillosus* Jones** Zoe 2: 241. 1891. Fabaceae. = *A. flavus* Nutt. var. *argillosus* (Jones) Barneby Emery Co., Greene River, Jones sn, 1890 (POM!;US!;BRY!).

***Astragalus argophyllus* Nutt. var. *cnicensis* Jones** Rev. Astragalus 207. 1923. Fabaceae. = *A. argophyllus* var. *martinii* Jones Utah Co., Thistle, Jones sn, 1898 (POM!).

Astragalus arietinus **Jones** Proc. Calif. Acad. II. 5: 653. 1895. Fabaceae. = *A. cibarius* Sheld. Sanpete Co., Fairview, Jones 5544o, 1894 (POM!).

Astragalus asclepiadoides **Jones** Zoe 2: 238. 1891. Fabaceae. Grand Co., Cisco, Jones sn, 1889 (POM!).

Astragalus beckwithii **T. & G. var. *beckwithii*** Rep. U.S. Explor. & Surv. R.R. Pacific 2: 120. 1855. Fabaceae. Tooele Co.?, west of Lone Rock, Beckwith, 1854 (GH).

Astragalus beckwithii **T. & G. var. *purpureus*** **Jones** Zoe 3: 288. 1893. Fabaceae. Juab Co., Deep Creek Mts., Jones sn, 1891 (US!;POM!;BRY!;NY!).

Astragalus castaneiformis **var. *consobrinus*** **Barneby** Amer. Midl. Naturalist 41: 496. 1949. Fabaceae. = *A. consobrinus* (Barneby) Welsh Wayne Co., Bicknell, Ripley & Barneby 8605, 1947 (CAS!;RM!;NY!;UTC!).

Astragalus chamaeleuce **Gray in Ives var. *panguicensis*** **Jones** Proc. Calif. Acad. II. 5: 671. 1895. Fabaceae. = *A. argophyllus* var. *panguicensis* (Jones) Jones Garfield Co., Panguitch Lake, Jones 6023f, 1894 (POM!).

Astragalus chloodes **Barneby** Leafl. W. Bot. 5: 6. 1947. Fabaceae. Uintah Co., 6 mi se Jensen, Ripley & Barneby 7797, 1946 (CAS!;RM!;NY!;UTC!).

Astragalus cibarius **Sheld.** Bull. Geol. & Nat. Hist. Surv. Minnesota 9: 149. 1894. Fabaceae. Syn: *A. arietinus* Jones Utah Co., Utah Valley, Jones 1679, 1880 (MINN;POM!;US!;NY!).

Astragalus cicadae **var. *laccoliticus*** **Jones** Proc. Calif. Acad. II. 5: 672. 1895. Fabaceae. = *A. chamaeleuce* Gray Garfield Co., Henry Mts., Jones 5658q, 1894 (POM!).

Astragalus coltonii **Jones var. *aphyllus*** **Jones** Rev. Astragalus 71. 1923. Fabaceae. Syn: *A. coltonii* var. *coltonii* Sevier Co., near Richfield, Jones sn, 1898 (POM!).

Astragalus coltonii **Jones var. *coltonii*** Zoe 2: 237. 1891. Fabaceae. Syn:*Astragalus coltonii* var. *aphyllus* Jones Carbon Co., Castle Gate, Jones sn, 1889 (POM!;US!;NY!).

Astragalus coltonii **Jones var. *moabensis*** **Jones** Contr. W. Bot. 8: 11. 1898. Fabaceae. Syn: *Homalobus canovirens* Rydb. San Juan Co., Monticello, Eastwood 9, 1892 (POM!).

Astragalus convallarius **Greene var. *finitimus*** **Barneby** Leafl. W. Bot. 7: 192. 1954. Fabaceae. Washington Co., 3 mi s Enterprise, Ripley & Barneby 4967, 1942 (CAS!).

Astragalus cottamii **Welsh** Rhodora 72: 189. 1970. Fabaceae. San Juan Co., e Clay Hills Divide, Welsh 5207, 1966 (BRY!;NY!;ISC!).

Astragalus cronquistii **Barneby** Mem. New York Bot. Gard. 13: 258. 1964. Fabaceae. San Juan Co., w side Comb Wash, Cronquist 9123, 1961 (NY!;UTC!).

Astragalus cymboides **Jones** Proc. Calif. Acad. II, 5: 650. 1895. Fabaceae. Syn: *A. amphyoxys* var. *cymbellus* Jones Emery Co., Huntington, Jones 5464j, 1894 (POM!;US!;NY!).

Astragalus desereticus **Barneby** Mem. New York Bot. Gard. 13: 635. 1964. Fabaceae. Sanpete Co., Indianola, Tidestrom 2249, 1909 (GH).

Astragalus desperatus **Jones var. *desperatus*** Zoe 2: 243. 1891. Fabaceae. Grand Co., near Cisco, Jones sn, 1890 (US!;RM!;BRY!).

Astragalus desperatus **Jones var. *petrophilus*** **Jones** Rev. Astragalus 204. 1923. Fabaceae. Emery Co., San Rafael Swell, Jones sn, 1914 (POM!;RM!;BRY!;NY!).

Astragalus detritalis **Jones** Contr. W. Bot. 13: 9. 1910. Fabaceae. Syn: *A. spectabilis* C.L. Porter Duchesne Co., near Theodore, Jones sn, 1908 (POM!;BRY!;NY!).

Astragalus diehlii **Jones** Rev. Astragalus 194. 1923. Fabaceae. = *A. flexuosus* var. *diehlii* (Jones) Barneby Carbon Co., Farnham, Jones sn, 1898 (POM!;RM!;NY!;BRY!;UTC!).

Astragalus dodgeanus **Jones** Zoe 3: 289. 1893. Fabaceae. = *A. wingatanus* Wats. Grand Co., Thompsons Springs, Jones sn, 1891 (POM!;BRY!;NY!).

Astragalus duchesnensis **Jones** Contr. W. Bot. 13: 6. 1910. Fabaceae. Duchesne Co., Theodore to Myton, Jones sn, 1908 (POM!;CAS!;RM!;BRY!;US!;NY!).

Astragalus ensiformis **Jones var. *gracilior*** **Barneby** Proc. Calif. Acad. IV. 25: 158. 1944. Fabaceae. = *A. ensiformis* Jones Washington Co., s Veyo, Ripley & Barneby 4951, 1942 (CAS!;NY!).

Astragalus episcopus **Wats.** Proc. Amer. Acad. 10: 345. 1875. Fabaceae. Kane (?) Co., Bishop sn, 1872 (GH;US!;NY!).

Astragalus equisolensis **Neese & Welsh** Rhodora 83: 457. 1981. Fabaceae. Uintah Co, s Jensen, Neese & Welsh 7380, 1979 (BRY!;NY!;US!;POM!;UTC!).

Astragalus eremiticus **Sheld.** Bull. Geol. & Nat. Hist. Surv. Minnesota 9: 161. 1894. Fabaceae. Washington Co., Beaver Dam Mountains, Parry 45, 1874 (MINN; US!;ISC!;NY!).

Astragalus eurekensis **Jones** Contr. W. Bot. 8: 12. 1898. Fabaceae. Syn: *Xylophacos medius* Rydb. Juab Co., Eureka, Jones sn, 1891 (POM!;BRY!).

Astragalus flavus **Nutt. in T. & G. var. *candicans*** **Gray** Proc. Amer. Acad. 12: 54. 1876. Fabaceae. Syn: *A. confertiflorus* Gray Sevier Co., near Richfield, Ward 246, 1875 (GH;NY!).

Astragalus hamiltonii **C.L. Porter** Rhodora 54: 159. 1952. Fabaceae. Uintah Co., 5 mi sw Vernal, Hamilton & Beath sn, 1952 (RM!).

Astragalus harrisonii **Barneby** Mem. New York Bot. Gard. 13: 271. 1964. Fabaceae. Wayne Co., near Fruita, Barneby 13131, 1961 (CAS!;US!;BRY!;NY!;UTC!).

Astragalus haydenianus **Gray ex Brandegee var. *major*** **Jones** Zoe 2: 240. 1891. Fabaceae. = *A. bisulcatus* var. *major* (Jones) Welsh Kane Co., Johnson, Jones sn, 1890 (POM!;BRY!;NY!).

Astragalus ibapensis **Jones** Zoe 3: 290. 1893. Fabaceae. = *A. diversifolius* Gray Juab Co., Deep Creek Mts., Jones sn, 1891 (POM!).

Astragalus iselyi **Welsh** Great Basin Naturalist 34: 305. 1974. Fabaceae. San Juan Co., Brumley Ridge, Welsh 10970, 1971 (BRY!;UT!;POM!;UTC!;ISC!).

Astragalus jejunus **Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 73. 1871. Fabaceae. Summit (?) Co., Bear River Valley, Watson 279, 1869 (NY!).

Astragalus junceus **var. *attenuatus*** **Jones** Rev. Astragalus 76. 1923. Fabaceae. = *A. convallarius* Greene Carbon Co., Price, Jones sn, 1898 (POM!;BRY!;NY!).

Astragalus lentiginosus **Dougl. ex Hook. var. *chartaceus*** **Jones** Proc. Calif. Acad. II. 5: 673. 1895. Fabaceae. = *A. lentiginous* var. *araneosus* (Sheld.) Barneby Sanpete Co., Ephriam, Jones 5627m, 1894 (POM!).

Astragalus lentiginosus **Dougl. ex Hook. var. *pohlii*** **Welsh & Barneby** Isleya 2: 1. 1981. Fabaceae. Tooele Co., 4.5 mi N Vernon, Welsh et al. 16743, 1978 (BRY!;NY!;UTC!).

Astragalus lentiginosus **Dougl. ex Hook.** var. ***vitreus*** **Barneby** Leafl. W. Bot. 4: 119. 1945. Fabaceae. Washington Co., 5 mi w Leeds, Maguire & Blood 4413, 1933 (UTC!).

Astragalus lentiginosus **Dougl. ex Hook.** var. ***wahweapensis*** **Welsh** Great Basin Naturalist 38: 286. 1978. Fabaceae. Kane Co., Four Mile Bench, Welsh 12426, 1974 (BRY!;ISC!).

Astragalus limnocharis **Barneby** Leafl. W. Bot. 4: 236. 1946. Fabaceae. Kane Co., Navajo Lake, Maguire 19474, 1940 (NY!;RM!;UTC!).

Astragalus nidularius **Barneby** Leafl. W. Bot. 8: 16. 1956. Fabaceae. San Juan Co., White Canyon, Barneby 12778, 1955 (CAS!;US!;RM!;NY!;UT!;UTC!).

Astragalus palans **Jones** Zoe 4: 37. 1893. Fabaceae. = *A. lentiginosus* var. *palans* (Jones) Jones San Juan Co., Montezuma Canyon, Eastwood sn, 1892 (RM!;NY!).

Astragalus peabodianus **Jones** Zoe 3: 295. 1893. Fabaceae. = *A. pubentissimus* var. *peabodianus* (Jones) Welsh Grand Co., Thompsons Springs, Jones sn, 1891 (POM!).

Astragalus perianus **Barneby** Mem. New York Bot. Gard. 13(2): 973. 1964. Fabaceae. Piute Co, n Bullion Creek, Rydberg & Carlton 7104, 1905 (NY!;RM!;US!).

Astragalus pictus var. ***angustus*** **Jones** Zoe 4: 37. 1893. Fabaceae. = *A. ceramicus* Sheld. San Juan Co., Montezuma Canyon, Eastwood 7, 1892 (POM!;US!).

Astragalus pictus var. ***magnus*** **Jones** Rev. Astragalus 109. 1923. Fabaceae. = *A. ceramicus* Sheld. Washington Co., Silver Reef, Jones 5160, 1894 (POM!;RM!).

Astragalus pinonis **Jones** Contr. W. Bot. 8: 14. 1898. Fabaceae. Beaver Co., Frisco, Jones sn, 1880 (POM!).

Astragalus preussii **Gray** var. ***latus*** **Jones** Zoe 4: 36. 1893. Fabaceae. = *A. preussii* Gray var. *preussii* Emery Co., Green River, Jones sn, 1891 (NY).

Astragalus preussii **Gray** var. ***sulcatus*** **Jones** Zoe 4: 37. 1893. Fabaceae. = *A. eastwoodiae* Jones Southeast Utah, Cane Spring, Eastwood sn, 1892 (CAS!;BRY!;NY!;POM!).

Astragalus rafaelensis **Jones** Rev. Astragalus 146. 1923. Fabaceae. Emery Co., Cedar Mt., Jones sn, 1915 (POM!;CAS!;RM!;BRY!;NY!;UTC!).

Astragalus sabulosus **Jones** Zoe 2: 239. 1891. Fabaceae. Grand Co., Cisco, Jones sn, 1890 (POM!;BRY!).

Astragalus saurinus **Barneby** Leafl. W. Bot. 8: 17. 1956. Fabaceae. Uintah Co, 6 mi N Jensen, Holmgren & Tillett 9527, 1953 (NY!;CAS!;RM!).

Astragalus serpens **Jones** Proc. Calif. Acad. II, 5: 641. 1895. Fabaceae. Wayne Co., Loa Pass, Jones 5639i, 1894 (POM!;US!;NY!).

Astragalus sesquiflorus **Wats.** Proc. Amer. Acad. 10: 345. 1875. Fabaceae. Kane Co., near Kanab?, Bishop sn, 1873 (GH;US!).

Astragalus sileranus **Jones** Zoe 2: 242. 1891. Fabaceae. = *A. subcinereus* Gray Kane Co., Sink Valley, Jones sn, 1890 (POM!;CAS!;US!;BRY!;NY!).

Astragalus sileranus **Jones** var. ***caraicus*** **Jones** Proc. Calif. Acad. II. 5: 642. 1895. Fabaceae. = *A. subcinereus* Gray Kane (?) Co., Elk Ranch, Jones 6036, 1894 (POM!;BRY!).

Astragalus spectabilis **C.L. Porter** Rhodora 54: 160. 1952. Fabaceae. = *A. detritalis* Jones Uintah Co., 5 mi sw Vernal, Porter 5309, 1950 (RM!;CAS!;BRY!;POM!;NY!).

Astragalus stocksii **Welsh** Great Basin Naturalist 34: 307. 1974. Fabaceae. = *A. henrimontanensis* Welsh Garfield Co., Henry Mts., Welsh 11740, 1972 (BRY!;ISC!).

Astragalus straturensis **Jones** Contr. W. Bot. 8: 19. 1898. Fabaceae. Washington Co., Silver Reef, Jones 5175, 1894 (POM!;US!;RM!;NY!;BRY!).

Astragalus striatiflorus **Jones** Proc. Calif. Acad. II. 7: 643. 1895. Fabaceae. Washington Co., Springdale, Jones 6080k, 1894 (POM).

Astragalus subcinereus **Gray** var. ***basalticus*** **Welsh** Great Basin Naturalist 38: 302. 1978. Fabaceae. Sevier Co., 10 mi s Fremont Jct., Welsh et al. 6447, 1967 (BRY!;ISC!).

Astragalus subcinereus **Gray** var. ***subcinereus*** Proc. Amer. Acad. 13: 366. 1878. Fabaceae. Syn: *A. sileranus* Jones; *A. sileranus* var. *caraicus* Jones Southern Utah, (Northern Arizona ?), Palmer 117 1877 (US!;ISC!;NY!).

Astragalus tegetarius **Wats.** var. ***rotundus*** **Jones** Proc. Calif. Acad. II. 5: 650. 1895. Fabaceae. = *A. kentrophyta var. implexus* (Canby) Barneby Wayne Co., near Loa, Jones 5649b, 1894 (POM!;UC!).

Astragalus tetrapterus **Gray** Proc. Amer. Acad. 13: 369. 1878. Fabaceae. Washington Co., 25 mi n St. George, Palmer 111, 1877 (NY!;ISC!).

Astragalus thompsonae **Wats.** Proc. Amer. Acad. 10: 344. 1875. Fabaceae. = *A. mollissimus* var. *thompsonae* (Wats.) Barneby Kane Co., Kanab, Thompson sn, 1872 (GH;US!).

Astragalus ursinus **Gray** Proc. Amer. Acad. 13: 367. 1878. Fabaceae. = *A. lentiginosus* var. *ursinus* (Gray) Barneby Iron (?) Co., Bear Valley, Palmer sn, 1877 (GH!;NY!;ISC!).

Astragalus wardii **Gray** Proc. Amer. Acad. 12: 55. 1876. Fabaceae. Garfield (?) Co., Aquarius Pl., Ward 424, 1875 (GH;US!;NY!).

Astragalus woodruffii **Jones** Rev. Astragalus 77. 1923. Fabaceae. Emery Co., San Rafael Swell, Jones sn, 1914 (POM!;US!;CAS!;RM!;BRY!;NY!;UTC!).

Astragalus zionis **Jones** Proc. Calif. Acad. II, 5: 652. 1895. Fabaceae. Washington Co., Springdale, Jones 5261w, 1894 (POM!;US!;RM!;BRY!).

Atriplex bonnevillensis **C.A. Hanson** Stud. Syst. Bot. (BRY) 1: 2. 1962. Chenopodiaceae. Millard Co., Pine Valley playa, Hanson 354, 1960 (BRY!;UTC!).

Atriplex caput-medusae **Eastw.** Proc. Calif. Acad. II. 6: 316. 1896. Chenopodiaceae. = *A. argentea* var. *caput-medusae* (Eastw.) Fosberg San Juan Co., Recapture Creek, Eastwood 116, 1895 (US!;CAS!).

Atriplex cornuta **Jones** Proc. Calif. Acad. II. 5: 718. 1895. Chenopodiaceae. = *A. saccaria* Wats. Emery Co., Green River, Jones 5481, 1894 (POM!;US!).

Atriplex cuneata **A. Nels.** Bot. Gaz. 34: 357. 1902. Chenopodiaceae. Emery Co., Emery, Jones 5443, 1894 (US!;RM!).

Atriplex cuneata **A. Nels.** ssp. ***introgressa*** **C.A. Hanson** Stud. Syst. Bot. (BRY) 1: 4. 1962. Chenopodiaceae. Carbon Co., Wellington, Hanson 346, 1961 (BRY!;POM!).

Atriplex garrettii **Rydb.** Bull. Torrey Bot. Club 39: 312. 1912. Chenopodiaceae. Grand Co., Moab vicinity, Rydberg & Garrett 8465, 1911 (NY!;US!;UT!).

Atriplex graciliflora **Jones** Proc. Calif. Acad. II, 5: 717. 1895. Chenopodiaceae. Wayne Co., Blue Valley, Jones 5697, 1894 (POM!;US!;RM!;BRY!).

Atriplex nuttallii Wats. var. ***utahensis*** **Jones** Contr. W. Bot. 11: 19. 1903. Chenopodiaceae. = *A. tridentata* Kuntze Salt Lake Co., Salt Lake City, Jones 1760, 1879? (UC).

Atriplex rydbergii **Standl.** N. Amer. Fl. 21: 47. 1916. Chenopodiaceae. = *A. argentea* var. *argentea* San Juan (?) Co., s Moab, Rydberg & Garrett 9110, 1911 (US!;NY!).

Atriplex subdecumbens **Jones** Proc. Calif. Acad. II. 5: 716. 1895. Chenopodiaceae. = *A. truncata* (Torr.) Gray Sevier Co., Fish Lake, Jones 5745, 1894 (POM!;US!).

Atriplex tenuissima **A. Nels.** Bot. Gaz. 34: 359. 1902. Chenopodiaceae. = *A. wolfii* Wats. Sanpete Co., Gunnison, Jones 6525, 1900 (US!;RM!;POM!;NY!).

Atriplex tridentata **Kuntze** Rev. Gen. 2: 546. 1891. Chenopodiaceae. Syn: *A. nuttallii* var. *utahensis* Jones Box Elder Co., Corinne, Kuntze 3084, 1874 (NY!).

Atriplex welshii **C. A. Hanson** Stud. Syst. Bot. (BRY) 1: 1. 1962. Chenopodiaceae. Grand Co., 4 mi s Cisco, Hanson 322, 1961 (BRY!;ISC!).

Atropis laevis var. ***rigida*** **Beal** Grasses N. Amer. 2: 578. 1896. Poaceae. = *Poa canbyi* (Scribn.) Howell Tooele Co., Lake Point, Jones 1021, 1879(US!).

Aulospermum minimum **Mathias** Ann. Missouri Bot. Gard. 17: 353. 1930. Apiaceae. = *Cymopterus minimus* (Mathias) Mathias Iron Co., Cedar Breaks, Mathias 723, 1929 (MO;CAS!;BRY!).

Aulospermum rosei **Jones in Coult. & Rose** Contr. U.S. Natl. Herb. 7: 179. 1900. Apiaceae. = *Cymopterus rosei* (Jones) Jones Sevier Co., Richfield, Jones 30, 1899 (US!;POM!).

Bahia desertorum **Jones** Zoe 2: 249. 1891. Asteraceae. = *Platyschkuhria integrifolia* var. *deserertorum* (Jones) Ellison Grand Co., Cisco, Jones sn, 1890 (US!;POM!).

Bahia ourolepis **Blake** Proc. Biol. Soc. Washington 35: 175. 1922. Asteraceae. = *Platyschkuhria oblongifolia* (Gray) Rydb. Emery Co., Green River, Jones 5482#1 1894 (US!;POM!).

Balsamorhiza hispidula **Sharp** Ann. Missouri Bot. Gard. 22: 137. 1935. Asteraceae. = *B. hookeri* var. *hispidula* (Sharp) Cronq. Tooele Co., Lake Point, Jones 1727, 1880 (UT!;UTC!).

Batidophaca sabinarum **Rydb.** N. Amer. Fl. 24: 320. 1929. Fabaceae. = *Astragalus argophyllus* var. *panguicensis* (Jones) Jones Iron Co., Cedar Canyon, Garrett 2660, 1920 (NY!).

Betula utahensis **Britt.** Bull. Torrey Bot. Club 31: 165. 1904. Betulaceae. = *B. occidentalis x B. papyrifera* Salt Lake Co., City Creek Canyon, Stokes sn, 1900 (NY!).

Bigelovia douglasii var. ***spathulata*** **Jones** Proc. Calif. Acad. II, 5: 690. 1895. Asteraceae. = *Chrysothamnus viscidiflorus* var. *pumilus* (Nutt.) Jeps. Sevier Co., Fish Lake, Jones 5758m, 1894 (POM;US!).

Bigelovia glareosa **Jones** Zoe 2: 247. 1891. Asteraceae. = *C. nauseosus* (Pallas) Britt. var. *glareosa* (Jones) Welsh Piute Co., Marysvale, Jones sn, 1890 (POM).

Bigelovia howardii var. ***attenuata*** **Jones** Proc. Calif. Acad. II, 5: 691. 1895. Asteraceae. = *Chrysothamnus parryi* var. *attenuatus* (Jones) Kittell Piute Co., Marysvale, Jones 5912, 1894 (US!;RM!;NY!).

Bigelovia leiosperma **Gray** Syn. Fl. 1(2): 129. 1884. Asteraceae. = *Chrysothamnus nauseosus* var. *leiosperma* (Gray) Hall Washington Co., St. George, Palmer sn, 1875 (NY!;BRY!).

Bigelovia leiosperma **Gray** var. ***abbreviata*** **Jones** Proc. Calif. Acad. II, 5: 693. 1895. Asteraceae. = *Chrysothamnus nauseosus* (Pallas) Britt. Sevier Co., Clear Creek Canyon, Jones 6105, 1894 (POM!;US!;NY!).

Bigelovia menziesii var. ***scopulorum*** **Jones** Proc. Calif. Acad. II, 5: 692. 1895. Asteraceae. = *Haplopappus scopulorum* (Jones) Blake Iron Co., near Cedar City, Jones 5204v, 1894 (POM!;US!).

Bigelovia turbinata **Jones** Proc. Calif. Acad. II, 5: 691. 1895. Asteraceae. = *Chrysothamnus nauseosus* var. *turbinatus* (Jones) Blake Garfield (?) Co., Canaan Ranch, Jones 6066c, 1894 (POM!;US!).

Brickellia atractyloides **Gray** Proc. Amer. Acad. 8: 290. 1870. Asteraceae. Utah?, Colorado River, Palmer sn, 1870 (US!).

Brickellia linifolia **D.C. Eaton** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 137. 1871. Asteraceae. = *B. oblongifolia* Wats. var. *linifolia* (D.C. Eaton) Robins. Utah Co., Jordan Valley, American Fork, Watson 493, 1869 (US!;CAS!).

Brickellia watsonii **Robins.** Mem. Gray Herb. 1: 42. 1917. Asteraceae. = *B. microphylla* var. *watsonii* (Robins.) Welsh Utah Co., American Fork Canyon, Watson 494, 1869 (US!;NY!).

Buddleja utahensis **Cov.** Proc. Biol. Soc. Washington 7: 69. 1892. Loganiaceae. Washington Co., St. George, Palmer 400, 1877 (US!;NY!;BRY!;ISC!).

Caesalpinia repens **Eastw.** Zoe 4: 116. 1893. Fabaceae. = *Hoffmanseggia repens* (Eastw.) Cockerell Grand Co., Courthouse Wash, Eastwood sn, 1892 (CAS!;US!).

Calamagrostis scopulorum **Jones** Proc. Calif. Acad. II, 5: 722. 1895. Poaceae. Syn: *C. scopulorum* var. *lucidulum* Kearney Washington Co., Springdale, Jones 6075, 1894 (POM!;NY!).

Calamagrostis scopulorum **Jones** var. ***lucidula*** **Kearney** USDA Agrostol. Bull. 11: 33. 1898. Poaceae. = *C. scopulorum* Jones Salt Lake Co., Alta, Jones 1145, 1879 (POM!;NY!;BRY!;UTC!).

Calochortus aureus **Wats.** Amer. Naturalist 7: 303. 1873. Liliaceae. Syn: *C. nuttallii* var. *aureus* (Wats.) Ownbey Kane (?) Co., "S. Utah" Thompson, 1872 (US!).

Calochortus flexuosus **Wats.** Amer. Naturalist 7: 303. 1873. Liliaceae. Kane (?) Co., "S. Utah or N. Arizona", Thompson sn, 1872 (GH).

Camassia quamash (Pursh) **Greene** ssp. ***utahensis*** **Gould** Amer. Midl. Naturalist 28: 740. 1942. Liliaceae. = *C. quamash* (Pursh) Greene Cache Co., Blacksmith Canyon, Maguire & Maguire 3265, 1932 (?).

Camissonia gouldii **Raven** Contr. U.S. Natl. Herb. 37: 368. 1969. Onagraceae. Washington Co., N of St. George, Gould 1423, 1941 (US!;CAS!).

Capnodes brachycarpum **Rydb.** Bull. Torrey Bot. Club 34: 426. 1907. Fumariaceae. = *Corydalis caseana* ssp. *brachycarpa* (Rydb.) M. Ownbey Salt Lake Co., Alta, Jones 1197, 1879 (NY!;US!;RM!;POM!;BRY!;UTC!).

Cardamine cordifolia **Gray** var. ***pubescens*** **Gray ex Schulz** Engl. Bot. Jahrb. 32: 439. 1903. Brassicaceae. = *C. cordifolia* Gray Garfield (?) Co., Thousand Lake Mtn., Ward 396, 1875 (US!).

Cardamine palustris var. ***jonesii*** **Kuntze** Rev. Gen. 1: 125. 1891. Brassicaceae. = *Rorippa curvipes* var. *curvipes* Salt Lake Co., City Creek Canyon, Jones 1352, 1879 (POM!;NY!).

***Cardamine uintahensis* F.J. Hermann** Rhodora 36: 410. 1934. Brassicaceae. = *C. cordifolia* Gray Summit Co., Mt. Elizabeth Ridge, Hermann 5894, 1933 (GH).

***Carduus lacerus* Rydb.** Bull. Torrey Bot. Club 37: 543. 1910. Asteraceae. = *Cirsium scariosum* Nutt. Wasatch Co., near Midway, Carlton & Garrett 6732, 1905 (RM!;NY!).

***Carduus olivescens* Rydb.** Bull. Torrey Bot. Club 37: 544. 1910. Asteraceae. = *C. scariosum* Nutt. Garfield Co., Aquarius Plateau, Rydberg & Carlton 7450, 1905 (NY!).

***Carex campylocarpa* T.H. Holm ssp. *affinis* Maguire & Holmgren** Leafl. W. Bot. 4: 262. 1946. Cyperaceae. = *C. scopulorum* T.H. Holm Juab Co., Indian Farm Creek, Maguire & Holmgren 21947, 1943 (NY!;US!;CAS!;UTC!).

***Carex canescens* L. var. *dubia* Bailey** Bot. Gaz. 9: 119. 1884. Cyperaceae. = *C. canescens* L. Summit (?) Co., Bear River Canyon, Watson 1231A, 1869 (NY!).

***Carex epapillosa* Mack. in Rydb.** Fl. Rocky Mts. 138. 1060. 1917. Cyperaceae. = *C. atrata* L. Piute Co., Marysvale, Jones 5345, 1894 (NY!;US!;POM!;BRY!).

***Carex interimus* Maguire** Brittonia 5: 200. 1944. Cyperaceae. = *C. aquatilis* Wahl. Cache Co, Tony Grove Lake, Maguire 16098, 1938 (NY!;CAS!;US!;UTC!).

***Carex pelocarpa* F. Hermann** Rhodora 39: 492. 1937. Cyperaceae. = *C. nova* Bailey Summit Co., Lamotte Peak, Hermann 5983, 1933 (NY!;CAS!).

***Carex rachillis* Maguire** Brittonia 5: 199. 1944. Cyperaceae. = *C. subnigricans* Stacey Summit Co, Gilbert Peak, Maguire et al, 14668, 1936 (NY!;US!;CAS!;UTC!).

***Carex vernacula* Bailey var. *hobsonii* Maguire** Brittonia 5: 199. 1944. Cyperaceae. = *C. neurophora* Mack. Cache Co., Bear River Range, Maguire et al 14013, 1936 (NY!;CAS!;US!;UTC!).

***Carum garrettii* A. Nels. in Coult. & Rose** Contr. U.S. Natl. Herb. 12: 443. 1909. Apiaceae. = *Perideridia gairdneri* (H. & A.) Mathias Salt Lake (?) Co., Wasatch Mts., Garrett 2053, 1906 (US!;NY!).

***Castilleja aquariensis* N. Holmgren** Bull. Torrey Bot. Club 100: 87. 1973. Scrophulariaceae. Garfield Co., Aquarius Plateau, N. & P. Holmgren 4726, 1970 (NY!;US!;BRY!;UTC!).

***Castilleja arcuata* Rydb.** Bull. Torrey Bot. Club 34: 35. 1907. Scrophulariaceae. = *C. linariifolia* Benth. Sevier Co., Fish Lake, Rydberg & Carlton 7508, 1905 (NY!;RM!;US!).

***Castilleja flava* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 230. 1871. Scrophulariaceae. Summit (?) Co., Upper Bear River Valley, Watson 813, 1869 (US!;NY!).

***Castilleja leonardii* Rydb.** Bull. Torrey Bot. Club 34: 36. 1907. Scrophulariaceae. Utah Co., American Fork Canyon, Leonard 151, 1885 (NY!).

***Castilleja parvula* Rydb.** Bull. Torrey Bot. Club 34: 40. 1907. Scrophulariaceae. Piute Co., Bullion Creek, Rydberg & Carlton 7158, 1905 (NY!;US!).

***Castilleja revealii* N. Holmgren** Bull. Torrey Bot. Club 100: 87. 1973. Scrophulariaceae. Garfield Co., Bryce Canyon, Holmgren & Reveal 2017, 1965 (NY!;US!;BRY!;UT!;UTC!).

***Castilleja variabilis* Rydb.** Bull. Torrey Bot. Club 34: 37. 1907. Scrophulariaceae. = *C. miniata* Dougl. Salt Lake Co., Big Cottonwood Canyon, Rydberg 6773, 1905 (NY!;RM!).

***Castilleja viscida* Rydb.** Bull. Torrey Bot. Club 34: 32. 1907. Scrophulariaceae. Syn: *C. applegatei* var. *viscida* (Rydb.) Ownbey Salt Lake Co., Big Cottonwood Canyon, Rydberg & Carlton 6593, 1905 (NY!).

***Castilleja zionis* Eastw.** Leafl. W. Bot. 3: 91. 1941. Scrophulariaceae. Washington Co., Clear Creek, Eastwood & Howell 9227, 1941 (CAS!).

***Caulanthus crassicaulis* (Torr.) Wats. var. *glaber* Jones** Zoe 4: 266. 1893. Brassicaceae. Kane Co., Sink Valley, Jones sn, 1890 (POM!).

***Caulanthus crassicaulis* (Torr.) Wats. var. *major* Jones** Proc. Calif. Acad. II, 5: 623. 1895. Brassicaceae. Garfield Co., Henry Mts., Jones 5685, 1894 (POM!;US!;BRY!;NY!).

***Caulanthus divaricatus* Rollins** Contr. Gray Herb. II, 201: 8. 1971. Brassicaceae. = *Thelypodiopsis divaricata* (Rollins) Welsh & Reveal San Juan Co., 10 mi E of Hite, Cronquist 9033, 1961 (GH;NY!).

***Caulanthus hastatus* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 28. 1871. Brassicaceae. = *Chlorocrambe hastatus* (Wats.) Rydb. Salt Lake (?) Co., Wasatch Mts., Watson 114, 1869 (US!;NY!).

***Ceanothus fendleri* Gray var. *viridis* Jones** Proc. Calif. Acad. II, 5: 629. 1895. Rhamnaceae. = *C. fendleri* Gray Kane (?) Co., Elk Ranch, Jones 6032n, 1894 (POM!).

***Ceanothus martinii* Jones** Contr. W. Bot. 8: 41. 1898. Rhamnaceae. Syn: *C. utahensis* Eastw. Sanpete Co., Manti Canyon, Jones sn, 1895 (POM!;RM!;BRY!;NY!;UTC!).

***Ceanothus utahensis* Eastw.** Proc. Calif. Acad. IV. 16: 363. 1927. Rhamnaceae. = *C. martinii* Jones Wasatch Co., Soldier Summit, Eastwood 7689, 1918 (CAS!).

***Celtis villosula* Rydb.** Fl. Rocky Mts. ed 2. 1116. 1922. Ulmaceae. = *C. reticulata* Torr. Utah, without definite locality, Jones sn, 1894 (NY!).

***Cerastium variable* Goodding** Bot. Gaz. 37: 54. 1904. Caryophyllaceae. = *C. beeringianum* C. & S. Uintah Co., Dyer Mine, Goodding 1246, 1902 (US!;RM!;BRY!;NY!;UT!;ISC!).

***Cercis orbiculata* Greene** Feddes Repert. 11: 111. 1912. Fabaceae. = *C. occidentalis* var. *orbiculata* (Greene) Tidestr. Washington Co., Diamond Valley, Goodding 899, 1902 (US!;NY!).

***Cercocarpus flabellifolius* Rydb.** N. Amer. Fl. 22: 422. 1913. Rosaceae. = *C. montanus* Raf. Sevier Co., near Glenwood, Ward 122, 1875 (US!;NY!).

***Cercocarpus intricatus* Wats.** Proc. Amer. Acad. 10: 346. 1875. Rosaceae. Syn: *C. intricatus* var. *villosus* Schneid. Utah Co., American Fork Canyon, Watson 314, 1869 (US!;NY!).

***Cercocarpus intricatus* Wats. var. *villosus* Schneid.** Mitt. Deutsch. Dendr. Ges. 14: 129. 1905. Rosaceae. = *C. intricatus* Wats. Tooele (?) Co., Deep Creek, Jones sn, 1891 (US!).

***Cercocarpus ledifolius* Nutt. var. *intercedens* Schneid. f. *hirsutus* Schneid.** Mitt. Deutsch. Dendrol. Ges. 14: 129. 1905. Rosaceae. = *C. ledifolius* Nutt. Weber Co., Ogden Canyon, Pammel & Blackwood 3726, 1902 (ISC!;BRY!).

***Cercocarpus ledifolius* Nutt. var. *intercedens* f. *subglaber* Schneid.** Mitt. Deutsch. Dendr. Ges. 14: 128. 1905. Rosaceae. = *C. ledifolius* Nutt. Utah Co., Slate Canyon, Jones 5613b, 1894 (MO;NY!;US!;RM!;BRY!;POM!).

Cercocarpus parvifolius Woot. var. _minimus_ Schneid. Ill. Handb. Laubholzk. 1: 532. 1905. Rosaceae. = *C. montanus* Raf.? Utah ?.

Chaenactis brachiata Greene Leafl. Bot. Obs. & Crit. 2: 224. 1912. Asteraceae. = *C. douglasii* (Hook.) H. & A. Washington Co., Springdale, Jones 5261q, 1894 (US!;POM!).

Chaenactis brachiata Greene var. _stansburiana_ Stockwell Contr. Dudley Herb. 3: 111. 1940. Asteraceae. = *C. douglasii* (Hook.) H. & A. Tooele Co., Stansbury Island, Stansbury sn, 1850 (US;NY!).

Chaenactis douglasii (Hook.) H. & A. var. _alpina_ Gray Syn. Fl. N. Amer. 1(2): 341. 1884. = *C. alpina* (Gray) Jones Salt Lake Co., Alta, Jones 1232, 1879 (NY!;UTC!).

Cheirinia brachycarpa Rydb. Bull. Torrey Bot. Club 39: 325. 1912. Brassicaceae. = *Erysimum asperum* Nutt. San Juan Co., Abajo Mts., Rydberg & Garrett 9713, 1911 (NY!;US!;UT!).

Chrysopsis caespitosa Jones, not Nutt. Proc. Calif. Acad. II, 5: 694. 1895. Asteraceae. = *Heterotheca jonesii* (Blake) Welsh & Atwood Washington Co., Springdale, Jones 5249u, 1894 (POM!;US!).

Chrysopsis villosa Nutt. var. _cinerascens_ Blake Proc. Biol. Soc. Washington 35: 173. 1922. Asteraceae. = *Heterotheca villosa* (Nutt.) Shinners Beaver Co., Beaver Canyon, Tidestrom 2873, 1901 (US!).

Chrysopsis villosa Nutt. var. _scabra_ Eastw. Proc. Calif. Acad. II, 6: 294. 1896. Asteraceae. = *Heterotheca villosa* (Nutt.) Shinners San Juan Co., Willow Creek, Eastwood 38, 1895 (CAS!).

Chrysothamnus marianus Rydb. Bull. Torrey Bot. Club 37: 131. 1910. Asteraceae. = *C. viscidiflorus* var. *puberulus* (D.C. Eaton) Jeps. Piute Co., near Marysvale, Rydberg & Carlton 6993, 1905 (US;RM!;NY!).

Chrysothamnus nauseosus (Pallas) Britt. ssp. _iridis_ L.C. Anderson Great Basin Naturalist 41: 311. 1981. Asteraceae. Sevier Co., Rainbow Hills, Welsh 19258, 1979 (BRY!;FSU!).

Chrysothamnus nauseosus (Pallas) Britt. var. _psilocarpus_ Blake J. Washington Acad. Sci. 27: 376. 1937. Asteraceae. Syn: *C. nauseosus* ssp. *psilocarpus* (Blake) L.C. Anderson Emery Co., Huntington Canyon, Garrett 7021, 1935 (US).

Chrysothamnus oliganthus A. Nels. Univ. Wyoming Publ. Bot. 1: 65. 1924. Asteraceae. = *C. nauseosus* var. *leiospermus* (Gray) Hall Washington Co., Zion National Park, Nelson 9975, 1922 (RM!).

Chrysothamnus salicifolius Rydb. Bull. Torrey Bot. Club 37: 130. 1910. Asteraceae. = *C. nauseosus* (Pallas) Britt. var. *salicifolius* (Rydb.) Hall Wasatch Co., Strawberry Valley, Leonard 288, 1883 (NY!;BRY!).

Chrysothamnus zionis A. Nels. Univ. Wyoming Publ. Bot. 1: 66. 1924. Asteraceae. = *C. nauseosus* var. *gnaphaloides* (Greene) Hall Washington Co., 20 mi N St. George, Nelson 9980, 1922 (RM!).

Cirsium barnebyi Welsh & Neese in Welsh Brittonia 33: 296. 1981. Asteraceae. Uintah Co., 1.5 mi e Ignacio, Welsh 19606, 1980 (BRY!;NY!;US!;MINN!).

Cirsium eriocephalum var. _leiocephalum_ D.C. Eaton Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 196. 1871. Asteraceae. = *C. eatonii* Robins.var. *eatonii* Summit? Co., Uinta Mts., Watson 691, 1869 (US!;NY!).

Cirsium lactucinum Rydb. Fl. Rocky Mts. 1010, 1068. 1917. Asteraceae. = *C. rydbergii* Petrak San Juan Co., Bluff, Rydberg & Garrett 10001, 1911 (NY!;US!;UT!).

Cirsium pulchellum (Greene) Woot. & Standl. var. _glabrescens_ Petrak Beih. Bot. Centr. 35(2): 511. 1917. Asteraceae. = *C. bipinnatum* (Eastw.) Petrak San Juan Co., Elk Mts., Rydberg & Garrett 9335, 1911 (US!).

Cirsium rydbergii Petrak Beih. Bot. Centralbl. 35(2): 315. 1917. Asteraceae. Syn: *C. lactucinum* Rydb. San Juan Co., Bluff, Rydberg & Garrett 10001, 1911 (US!;UT!;NY!).

Cirsium undulatum (Nutt.) Spreng. var. _albescens_ D.C. Eaton Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 194. 1871. Asteraceae. = *C. undulatum* (Nutt.) Spreng. Tooele Co., Stansbury Island, Watson 687, 1869 (US!).

Cirsium utahense Petrak Beih. Bot. Centr. 35(2): 470. 1917. Asteraceae. Washington Co., Silver Reef, Jones 5163q, 1894 (POM!;US!).

Clematis alpina ssp. _occidentalis_ var. _repens_ Kuntze Verh. Bot. Ver. Brandenb. 26: 161. 1885. Ranunculaceae. = *C. columbiana* (Nutt.) T. & G. Utah Co., American Fork, Jones 1887, 1880 (NY!;POM!).

Clematis douglassii ssp. _jonesii_ Kuntze Verh. Bot. Ver. Brandenb. 25: 180. 1886. Ranunculaceae. = *C. hirsutissima* Pursh Utah Co., American Fork Canyon, Jones 1351, 1880 (US!;POM!;NY!).

Clematis pseudotragene ssp. _wenderothioides_ Kuntze Verh. Bot. Ver. Brandenb. 26: 160. 1885. Ranunculaceae. = *C. columbiana* var. *columbiana* Kane Co., Kanab, Siler sn, 1873 (K).

Cleome integrifolia var. _angusta_ Jones Proc. Calif. Acad. II, 5: 625. 1895. Capparidaceae. = *C. serrulata* var. *angusta* (Jones) Tidestr. Piute Co., Marysvale, Jones 6057, 1894 (US!).

Cleomella cornuta Rydb. Bull. Torrey Bot. Club 30: 249. 1903. Capparidaceae. = *C. palmeriana* Jones Wayne Co., Caineville, Jones 5656, 1894 (US!;BRY!;RM!;NY!).

Cleomella nana Eastw. Bull. Torrey Bot. Club 30: 490. 1903. Capparidaceae. = *C. palmeriana* Jones Grand Co., S of Thompsons Spr., Eastwood sn, 1892 (CAS!;RM!).

Cleomella palmerana Jones Zoe 2: 236. 1891. Capparidaceae. Emery Co., Green River, Jones sn, 1890 (POM;US!).

Cnicus calcareus Jones Proc. Calif. Acad. II, 5: 704. 1895. Asteraceae. = *Cirsium calcareum* (Jones) Woot. & Standl. Garfield Co., Bromide Pass, Jones 5695bh, 1894 (POM!;BRY!;US!;NY!).

Cnicus clavatus Jones Proc. Calif Acad. II, 5: 704. 1895. Asteraceae. = *Cirsium clavatum* (Jones) Petrak Sevier Co., Fish Lake, Jones 5715, 1894 (POM!;BRY!;US!;NY!).

Cnicus nidulus Jones Proc Calif. Acad. II, 5: 705. 1895. Asteraceae. = *Cirsium nidulum* (Jones) Petrak Garfield Co., Paria, Jones 5290a, 1894 (POM!;US!;NY!).

Cnicus rothrockii var. _diffusus_ Eastw. Proc. Calif. Acad. II, 6: 303. 1896. Asteraceae. = *C. rothrockii* (Gray) Petrak San Juan Co., Willow Creek, Eastwood 65, 1895 (US!;CAS!).

Cogswellia cottamii Jones Contr. W. Bot. 16: 36. 1930. Apiaceae. = *Lomatium parryi* (Wats.) Macbr. Washington Co., Beaverdam Mts., Cottam et al. 4098, 1929 (BRY!;UT!).

Cogswellia millefolia **var.** ***depauperata*** Jones Contr. W. Bot. 12: 38. 1908. Apiaceae. = *Lomatium grayi* Coult. & Rose Tooele Co., Dugway, Jones sn, 1891 (US!;POM!;NY!).

Cogswellia minima Mathias Ann. Missouri Bot. Gard. 19: 497. 1932. Apiaceae. = *Lomatium minimum* (Mathias) Mathias Garfield Co., Bryce Canyon, Mathias 670, 1929 (MO;CAS!;NY!).

Coleosanthes garretti A. Nels. Proc. Biol. Soc. Washington 20: 38. 1907. Asteraceae. = *Brickellia grandiflora* (Hook.) Nutt. Salt Lake Co., City Creek Canyon, Garrett 1061, 1904 (RM!;UT!).

Collomia tenella Gray Proc. Amer. Acad. 8: 259. 1870. Polemoniaceae. Summit Co., Parleys Park, Watson 900, 1869 (NY!).

Coloptera jonesii Coult. & Rose Rev. N. Amer. Umbell. 49. 1888. Apiaceae. = *Cymopterus newberryi* (Wats.) Jones Beaver Co., Milford, Jones 1792, 1880 (POM!;UT!).

Comandra linearis Rydb. Fl. Rocky Mts. 818. 1066. 1917. Santalaceae. = *C. umbellata* var. *pallida* (DC.) Jones Emery Co., Green River, Tracy 716, 1887 (NY!).

Cordylanthus parryi Wats. in Parry Amer. Naturalist 9: 346. 1875. Scrophulariaceae. = *C. maritimus* ssp. *canescens* (Gray) Chuang & Heckard Washington Co., Parry 155, 1874 (US!;NY!;ISC!).

Corydalis engelmannii **var.** ***exaltata*** Fedde Feddes Repert. 11: 497. 1913. Fumariaceae. = *C. aurea* Willd. Grand (?) Co., La Sal Mts., Purpus 6550, 1897 (US!).

Coryphantha marstonii Clover Bull. Torrey Bot. Club 65: 412. 1938. Cactaceae. = *C. missouriensis* var. *marstonii* (Clover) L. Benson Garfield Co., Hells Backbone, Clover 1909, 1937 (?) (MICH).

Cowania stansburiana Torr. in Stansb. Explor. Great Salt Lake 386. 1852. Rosaceae. = *C. mexicana* D. Don Davis (?) Co., Great Salt Lake, Stansbury sn, 1850 (NY!).

Crassipes annuus Swallen Amer. J. Bot. 18: 685. 1931. Poaceae. = *Sclerochloa dura* (L.) Beauv. Davis (?) Co., between Salt Lake City & Ogden, Fallas sn, 1928 (US!).

Crepis aculeolata Greene Leafl. Bot. Obs. & Crit. 2: 86. 1910. Asteraceae. = *C. runcinata* var. *runcinata* Utah, Ward 606, 1875 (US!).

Crepis occidentalis Nutt. **var.** ***costatus*** Gray Geol. Surv. Calif. Bot. 1: 435. 1880. Asteraceae. = *C. occidentalis* Nutt. Tooele Co., Stansbury Island, Watson 715, 1869 (US!).

Cressa erecta Rydb. Bull. Torrey Bot. Club 40: 466. 1913. Convolvulaceae. = *C. truxillensis* H.B.K. Salt Lake Co., Becks Hot Springs, Garrett 870f, 1905 (NY!).

Croton longipes Jones Proc. Calif. Acad. II, 5: 721. 1895. Euphorbiacea. Washington Co., 2 mi e Leeds, Jones 5213, 1894 (POM!;US!;CAS!;RM!;NY!).

Cryptantha barnebyi Johnst. J. Arnold Arb. 29: 240. 1948. Boraginaceae. Uintah Co., 30 mi s Ouray, Ripley & Barneby 8748, 1947 (GH;NY!).

Cryptantha compacta Higgins Great Basin Naturalist 28: 196. 1968. Boraginaceae. Millard Co., 8 mi w Desert Experimental Range, Higgins 1613, 1963 (BRY!;US!;POM!).

Cryptantha grahamii Johnst. J. Arnold Arb. 18: 23. 1937. Boraginaceae. Uintah Co., mouth Sand Wash, Graham 7924, 1933 (GH).

Cryptantha johnstonii Higgins Great Basin Naturalist 28: 195. 1968. Boraginaceae. Emery Co., 15 mi w Hwy 50–6, Higgins 1310, 1968 (BRY!;POM!;US!;NY!).

Cryptantha leptophylla Rydb. Bull. Torrey Bot. Club 36: 679. 1909. Boraginaceae. = *C. nevadensis* Nels. & Kennedy Washington Co., St. George, Palmer 350, 1877 (NY!).

Cryptantha ochroleuca Higgins Great Basin Naturalist 28: 197. 1968. Boraginaceae. Garfield Co., Red Canyon, Higgins 1788, 1968 (BRY!;US!).

Cryptantha rollinsii Johnst. J. Arnold Arb. 20: 391. 1939. Boraginaceae. Uintah Co., 22 mi s Ouray, Rollins 1715, 1937 (GH;US!;CAS!;RM!;UTC!).

Cuscuta denticulata Engelm. in Parry Amer. Naturalist 9: 348. 1875. Cuscutaceae. Washington Co., near St. George, Parry 205, 1874 (US!;NY!;ISC!;BRY!).

Cuscuta warneri Yuncker Brittonia 12: 38. 1960. Cuscutaceae. Millard (?) Co., Flowell, Warner sn, 1957 (US!;CAS!;BRY!;UT!;NY!;UTC!;ISC!).

Cycladenia jonesii Eastw. Leafl. W. Bot. 3: 159. 1942. Apocynaceae. = *C. humilis* var. *jonesii* (Eastw.) Welsh & Atwood Emery Co., San Rafael Swell, Jones sn, 1914 (CAS!;US!;BRY!).

Cymopterus basalticus Jones Contr W. Bot. 12: 16. 1908. Apiaceae. Beaver (?) Co., Wah Wah, Jones sn, 1906 (POM!;BRY!).

Cymopterus beckii Welsh & Goodrich in Welsh Brittonia 33: 297. 1981. Apiaceae. Wayne Co., Fruita, Beck sn, 1938 (BRY!).

Cymopterus corrugatus **var.** ***scopulicola*** Jones Contr. W. Bot. 14: 39. 1912. Apiaceae. = *C. coulteri* (Jones) Mathias Juab Co., Sevier Bridge, Jones sn, 1910 (POM!).

Cymopterus decipiens Jones Zoe 2: 247. 1891. Apiaceae. = *C. fendleri* Gray Grand Co., Cisco, Jones sn, 1891 (POM!;US!;NY!).

Cymopterus duchesnensis Jones Contr. W. Bot. 13: 12. 1910. Apiaceae. Duchesne Co., Myton, Jones sn, 1908 (CAS!;US!;RM!;POM!;BRY!).

Cymopterus higginsii Welsh Great Basin Naturalist 35: 377. 1976. Apiaceae. Kane Co., 17 mi e Glen Canyon City, Welsh 12740, 1975 (BRY!;NY!).

Cymopterus ibapensis Jones Zoe 3: 302. 1893. Apiaceae. Tooele (?) Co., Deep Creek Valley, Jones sn, 1891 (POM!;US!;RM!).

Cymopterus jonesii Coult. & Rose Rev. N. Amer. Umbell. 80. 1888. Apiaceae. Syn: *Aulospermum jonesii* (Coult. & Rose) Coult. & Rose Beaver Co., Frisco, Jones 1808, 1880 (US!;CAS!;POM!;RM!;NY!;UT!;UTC!).

Cymopterus longipes Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 124. 1871. Apiaceae. Syn: *Peucedanum lapidosum* Jones Salt Lake Co., near Salt Lake City, Watson 451, 1869 (US!;NY!).

Cynomarathrum latilobum Rydb. Bull. Torrey Bot. Club 40: 73. 1913. Apiaceae. = *Lomatium latilobum* (Rydb.) Mathias Grand Co., Wilson Mesa, Rydberg & Garrett 8371, 1911 (NY!;US!;UT!).

Cynomarathrum scabrum Coult. & Rose Contr. U.S. Natl. Herb. 7: 247. 1900. Apiaceae. = *Lomatium scabrum* (Coult. & Rose) Math. & Const. Beaver Co., Frisco, Jones 1864, 1880 (US!;CAS!;POM!;BRY!;NY!;UT!;UTC!).

Cystium stramineum Rydb. N. Amer. Fl. 24: 409. 1929. Fabaceae. = *Astragalus lentiginosus* var. *stramineus* (Rydb.) Barneby Washington Co., "S. Utah" Palmer sn, 1870 (NY!;US!).

Dalea epica Welsh Great Basin Naturalist 31: 90. 1971. Fabaceae. San Juan Co., 10 mi e Halls Crossing, Welsh 5205, 1966 (BRY!;NY!;ISC!).

Dalea johnsonii Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 64. 1871. Fabaceae. = *Psorothamnus fremontii* (Torr.) Barneby Washington Co., near St. George, Johnson sn, 1870 (GH).

Dalea nummularia Jones Contr. W. Bot. 18: 41. 1933. Fabaceae. = *Psorothamnus polyadenius* var. *jonesii* Barneby Emery Co., Green River, Jones sn, 1914 (US!;CAS!;NY!).

***Daucophyllum lineare* Rydb.** Bull. Torrey Bot. Club 40: 69. 1913. Apiaceae. = *Musineon lineare* (Rydb.) Mathias Cache Co., near Logan, Rydberg sn, 1895 (?).

***Delphinium abietorum* Tidestr.** Proc. Biol. Soc. Washington 27: 61. 1914. Ranunculaceae. = *D. occidentale* Wats. Sanpete (?) Co., Wasatch Plateau, Coville & Tidestrom 19, 1908 (US!).

***Delphinium coelestinum* Rydb.** Bull. Torrey Bot. Club 39: 320. 1912. Ranunculaceae. Syn: *D. amabile* Tidestr. (new name) = *D. scaposum* Greene Washington Co., St. George, Palmer 10, 1877 (NY!;US!).

***Delphinium leonardii* Rydb.** Bull. Torrey Bot. Club 39: 320. 1912 Ranunculaceae. = *D. andersonii* Gray Salt Lake Co., Garfield, Leonard 205, 1884 (NY!).

***Delphinium scopulorum* var. *attenuatum* Jones** Proc. Calif. Acad. II, 5: 617. 1895. Ranunculaceae. = *D. barbeyi* Huth. Piute Co., head Bullion Creek, Jones 5893d, 1894 (POM!;US!).

***Descurainia richardsonii* (Sweet) Schulz var. *macrosperma* Schulz** Pflanzenr. 4. Fam. 105(Heft 86): 319. 1924. Brassicaceae. = *D. richardsonii* var. *brevipes* (Nutt.) Welsh & Reveal Salt Lake Co., Alta, Jones 1117, 1879 (UTC!).

***Dicoria paniculata* Eastw.** Proc. Calif. Acad. II, 6: 298. 1896. Asteraceae. = *D. brandegei* Gray San Juan Co., McElmo & Recapture, Eastwood 51, 1895 (CAS!).

***Dicoria wetherillii* Eastw.** Proc. Calif. Acad. II, 6: 299. 1896. Asteraceae. = *D. brandegei* Gray (monstrous form?) San Juan Co., San Juan River, Wetherill sn, 1895 (CAS!).

***Distichlis maritima* var. *laxa* Holm** Bot. Gaz. 16: 277. 1891. Poaceae. = *D. stricta* (Torr.) Rydb. Utah, Lake Park, Tracy sn, 1887 (?).

***Dodecatheon zionense* Eastw.** Leafl. W. Bot. 2: 37. 1937. Primulaceae. = *D. pulchellum* (Raf.) Merr. Washington Co., Zion Canyon, Eastwood & Howell 1144, 1933 (CAS!).

***Draba apiculata* C.L. Hitchc.** Univ. Washington Publ. Biol. 11: 72. 1941. Brassicaceae. = *D. densifolia* var. *davisiae* (C.L. Hitchc.) Welsh & Reveal Summit Co., Uinta Mts, Payson & Payson 5048, 1926 (NY!;US!;RM!).

***Draba brachystylis* Rydb.** Bull. Torrey Bot. Club 29: 240. 1902. Brassicaceae. Salt Lake Co., Wasatch Mts., Alta, Jones 1357, 1879 (NY!;US!;CAS!;RM!;POM!).

***Draba maguirei* C.L. Hitchc. var. *burkei* C.L. Hitchc.** Univ. Washington Publ. Biol. 11: 70. 1941 Brassicaceae. Box Elder Co., Cottonwood Canyon, Burke 2968, 1932 (UTC!).

Draba maguirei* C.L. Hitchc. var. *maguirei Univ. Washington Publ. Biol. 11: 70. 1941. Brassicaceae. Cache Co., Bear River Range, Maguire et al. 14161, 1936 (WTU!;UTC!;NY!).

***Draba sobolifera* Rydb.** Bull. Torrey Bot. Club 30: 251. 1903. Brassicaceae. Syn: *D. uncinalis* Rydb. Piute Co., Tate Mine, Jones 5936, 1894 (NY!;US!;POM!).

***Draba spectabilis* Greene var. *glabrescens* Schulz** Pflanzenr. 4. Fam. 105 (Heft 89) : 84. 1927. Brassicaceae. = *D. spectabilis* Greene San Juan Co., LaSal Mts., Walker 275, 1912 (NY!;US!).

***Draba subalpina* Goodm. & Hitchc.** Ann. Missouri Bot. Gard. 19: 77. 1932. Brassicaceae. Iron Co., Cedar Breaks, Goodman & Hitchcock 1622, 1930 (NY!;RM!).

***Draba uncinalis* Rydb.** Bull. Torrey Bot. Club 30: 251. 1903. Brassicaceae. = *D. sobolifera* Rydb. Piute Co., Tate Mine, Jones 5940am, 1894 (US!;POM!).

***Draba valida* Goodding** Bot. Gaz. 37: 55. 1904. Brassicaceae. = *D. lanceolata* Royle Uintah Co., Dyer Mine, Goodding 1402, 1902 (US!;RM!).

***Draba zionensis* C.L. Hitchc.** Univ. Washington Publ. Biol. 11: 49. 1941. Brassicaceae. = *D. asprella* var. *zionensis* (C.L. Hitchc.) Welsh & Reveal Washington Co., Zion Canyon, Jones sn, 1923 (POM!;CAS!;BRY!).

***Drymocallis micropetala* Rydb.** N. Amer. Fl. 22: 375. 1908. Rosaceae. = *Potentilla glandulosa* var. *micropetala* (Rydb.) Welsh & Johnst. Salt Lake Co., City Creek Canyon, Rydberg 6153, 1905 (US!;NY!).

***Echinocactus johnsonii* Parry ex Engelm.** Rep. U.S. Geol. Explor 40th Parallel, Bot. 5: 117. 1871. Cactaceae. = *Neolloydia johnsonii* (Parry) L. Benson Washington Co., near St. George, Johnson sn, 1870? (GH?).

***Echinocactus whipplei* Engelm. & Bigel. var. *spinosior* Engelm.** Trans. Acad. Sci. St. Louis 2: 199. 1863. Cactaceae. = *Sclerocactus pubispinus* (Engelm.) L. Benson Utah, desert valley west of Camp Floyd, H. Engelmann sn, 1859 (MO).

***Echinocereus engelmannii* (Parry) Rumpler var. *purpureus* L. Benson** Cact. & Succ. J. (Los Angeles) 41: 127. 1969. Cactaceae. Washington Co., near St. George, Benson 13637, 1949 (POM).

***Edwinia macrocalyx* Small** N. Amer. Fl. 22: 176. 1905. Saxifragaceae. = *Jamesia americana* T. & G. Utah Co., American Fork Canyon, Watson 371, 1869 (US!).

***Elymus salina* Jones** Proc. Calif. Acad. II, 5: 725. 1895. Poaceae. Sevier Co., Salina Pass, Jones 5447, 1894 (RM!;BRY!;US!;NY!).

***Emmenanthe foliosa* Jones** Zoe 4: 278. 1893. Hydrophyllaceae. = *Phacelia salina* (A. Nels.) J.T. Howell Tooele (?) Co., Deep Creek, Jones sn, 1891 (POM!;US!).

***Encelia microcephala* Gray** Proc. Amer. Acad. 8: 657. 1873. Asteraceae. = *Helianthella microcephala* (Gray) Gray San Juan Co., Sierra Abajo, Newberry sn, 1859 (NY!).

***Encelia nudicaulis* Gray** Proc. Amer. Acad. 8: 656. 1873. Asteraceae. = *Enceliopsis nudicaulis* (Gray) A. Nels. Utah, Bishop sn, 1872 (US!).

***Epilobium palmeri* Rydb.** Bull. Torrey Bot. Club 31: 569. 1904. Onagraceae. = *E. saximontanum* Hausskn. Washington Co., (s. Utah), Palmer 156, 1877 (NY!).

***Epilobium tracyi* Rydb.** Bull. Torrey Bot. Club 40: 63. 1913. Onagraceae. = *E. brachycarpum* Presl Weber Co., Ogden, Tracy & Evans 547, 1887 (NY!).

***Eremocarya muricata* Rydb.** Bull. Torrey Bot. Club 36: 677. 1909. Boraginaceae. = *Cryptantha micrantha* (Torr.) Johnst. Southern Utah, Parry 164, 1874 (NY!;ISC!).

***Erigeron abajoensis* Cronq.** Brittonia 6: 168. 1947. Asteraceae. San Juan Co., Abajo Mts., Rydberg & Garrett 9755, 1911 (NY!;UT!).

Erigeron caespitosus **Nutt. var.** ***laccoliticus*** **Jones** Proc. Calif. Acad. II, 5: 696. 1895. Asteraceae. = *E. caespitosus* Nutt. Garfield Co., Henry Mts., Jones 5661, 1894 (POM!;US!).

Erigeron caespitosus **Nutt. var.** ***laccoliticus*** **Jones** Proc. Calif. Acad. II, 5: 696. 1895. Asteraceae. = *E. caespitosus* Nutt. Garfield Co., Henry Mts., Jones 5661, 1894 (POM!;US!).

Erigeron caespitosus **Nutt. var.** ***nauseosus*** **Jones** Proc. Calif. Acad. II, 5: 696. 1895. Asteraceae. = *E. nauseosus* (Jones) Cronq. Piute Co., Marysvale, Jones 5386, 1894 (POM!;US!;NY!).

Erigeron cinereus **var.** ***aridus*** **Jones** Proc. Calif. Acad. II, 5: 695. 1895. Asteraceae. = *E. divergens* T. & G. Washington Co., Silver Reef, Jones 5149v, 1894 (POM!;US!).

Erigeron controversus **Greene** Leafl. Bot. Obs. & Crit. 2: 206. 1912. Asteraceae. = *E. garretti* A. Nels. Salt Lake Co., Alta, Jones 1207, 1879 (US!;POM!).

Erigeron cronquistii **Maguire** Brittonia 5: 201. 1944. Asteraceae. Cache Co., Logan Canyon, Maguire 16681, 1939 (NY!;US!;UTC!).

Erigeron eatonii **Gray** Proc. Amer. Acad. 16: 91. 1880. Asteraceae. Summit Co., Uinta Mts., Watson 546, 1869 (US!;NY!).

Erigeron eatonii **Gray ssp.** ***typicus*** **Cronq. var.** ***molestus*** **Cronq.** Brittonia 6: 172. 1947. Asteraceae. = *E. eatonii* Gray Tooele Co., Mt. Deseret Peak, Stansbury Range, Maguire and Holmgren 21773, 1943 (NY!;UTC!).

Erigeron flagellaris **Gray var.** ***trilobatus*** **Maguire & Cronq.** Brittonia 6: 258. 1947. Asteraceae. = *E. proselyticus* Nesom Iron Co., Cedar Breaks, Maguire 14947, 1934 (NY!;UTC!).

Erigeron fruticetorum **Rydb.** Fl. Rocky Mts. 906, 1067. 1917. Asteraceae. = *E. formosissimus* Greene San Juan Co., La Sal Mts., Rydberg & Garrett 8912, 1911 (NY!).

Erigeron garrettii **A. Nels. in Coult. & Nels.** Man. Bot. Centr. Rocky Mts. 526. 1909. Asteraceae. Syn: *E. controversus* Greene Salt Lake Co., Big Cottonwood Canyon, Garrett 1310, 1905 (RM!;UT!).

Erigeron kachinensis **Welsh & Moore** Proc. Utah Acad. 45: 231. 1968. Asteraceae. San Juan Co, Natural Bridges, Welsh & Moore 2398, 1963 (BRY!;NY!).

Erigeron leiomerus **Gray** Syn. Fl. N. Amer. II. 1: 211. 1884. Asteraceae. Syn: *E. minusculus* Greene Summit Co., Uintas, Watson 504, 1869 (NY!).

Erigeron leiophyllus **Greene** Leafl. Bot. Obs. & Crit. 2: 218. 1912. Asteraceae. = *E. speciosus* var. *macranthus* (Nutt.) Cronq. Salt Lake Co., Fort Douglas, Jones sn, 1880 (US!;POM!).

Erigeron maguirei **Cronq.** Brittonia 6: 165. 1947. Asteraceae. Emery Co., Calf Spring Wash, Maguire 18459, 1940 (NY!;UTC!).

Erigeron mancus **Rydb.** Fl. Rocky Mts. 902, 1067. 1917. Asteraceae. Syn: *E. pinnatisectus* var. *insolens* Macbr. & Payson Grand Co., La Sal Mts., Rydberg & Garrett 8671, 1911 (NY!;US!;UT!;RM!).

Erigeron minusculus **Greene** Leafl. Bot. Obs. & Crit. 2: 8. 1909. Asteraceae. = *E. leiomeris* Gray Salt Lake Co., Big Cottonwood Canyon, Garrett, 1906 (UT?).

Erigeron pinnatisectus **A. Nels. var.** ***insolens*** **Macbr. & Payson** Contr. Gray Herb. II, 49: 79. 1917. Asteraceae. = *E. mancus* Rydb. Grand Co., La Sal Mts., Walker 271, 1912 (GH;MINN;RM!).

Erigeron pulvinatus **Rydb. non Wedd.** Fl. Rocky Mts. 911, 1067. 1917. Asteraceae. = *E. compactus* Blake Juab Co., Deep Creek, Jones sn, 1891 (US!;POM!;BRY!;NY!).

Erigeron pumilus **Nutt. ssp.** ***concinnoides*** **Cronq. var.** ***subglaber*** **Cronq.** Brittonia 6: 183. 1947. Asteraceae. San Juan Co., Monticello, Rydberg & Garrett 9141, 1911 (US!;RM!;UT!).

Erigeron religiosus **Cronq.** Brittonia 6: 258. 1947. Asteraceae. Washington Co., Clear Creek, Eastwood & Howell 6339, 1938 (CAS!;US!).

Erigeron sionis **Cronq.** Brittonia 6: 258. 1947. Asteraceae. Washington Co., Zion National Park, Pilsbry sn, 1925 (PH!).

Erigeron sparsifolius **Eastw.** Proc. Calif. Acad. II, 6: 297. 1896. Asteraceae. = *E. utahensis* Gray var. *sparsifolius* (Eastw.) Cronq. San Juan Co., Willow Creek, Eastwood 48, 1895 (CAS!).

Erigeron stenophyllus **D.C. Eaton** Rep. U.S. Geol. Explor. 40th Parallel, Bot 5: 152. 1871. Asteraceae. = *E. arenarioides* (D.C. Eaton) Rydb. Salt Lake Co., Cottonwood Canyon, Watson 547, 1869 (US!;NY!).

Erigeron stenophyllus **var.** ***tetrapleuris*** **Gray** Proc. Amer. Acad. 8: 650. 1873. Asteraceae. = *E. utahensis* Gray Kane Co., Kanab, Thompson sn, 1870 (GH).

Erigeron uintahensis **Cronq.** Bull. Torrey Bot. Club 70: 270. 1943. Asteraceae. Summit Co., Mill Creek, Payson 4894, 1936 (RM!;US!).

Erigeron ursinus **D.C. Eaton** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 148. 1871. Asteraceae. Summit Co., Bear River Canyon, Watson 534, 1869 (US!;NY!).

Erigeron vagus **Payson** Univ. Wyoming Publ. Bot. 1: 179. 1926. Asteraceae. Grand Co., LaSal Mts., Payson & Payson 4033, 1924 (US!;BRY!;RM!;NY!).

Eriogonum ammophilum **Reveal** Phytologia 23: 163. 1972. Polygonaceae. Millard Co., Ibex Warm Point, N. & P. Holmgren 4650, 1970 (US!;NY!;BRY!;UTC!).

Eriogonum aretioides **Barneby** Leafl. W. Bot. 5: 154. 1949. Polygonaceae. Garfield Co., Widtsoe, Ripley & Barneby 8570, 1947 (CAS!;NY!;BRY!).

Eriogonum aureum **Jones** Proc. Calif. Acad. II, 5: 718. 1895. Polygonaceae. = *E. corymbosum* var. *glutinosusm* (Jones) Jones Washington Co., St. George, Jones 6091, 1894 (POM!;US!;NY!).

Eriogonum batemanii **Jones** Contr. W. Bot. 11: 11. 1903. Polygonaceae. Carbon Co., Price Valley, Jones sn, 1903 (US!;POM!).

Eriogonum bicolor **Jones** Zoe 4: 281. 1893. Polygonaceae. Grand Co., Thompsons Spring, Jones sn, 1891 (US!;POM!;NY!).

Eriogonum biumbellatum **Rydb.** Bull. Torrey Bot. Club 39: 306. 1912. Polygonaceae. = *E. umbellatum* var. *subaridum* Stokes Sevier Co., Fish Lake, Rydberg & Carlton 7409, 1905 (US!;RM!;NY!).

Eriogonum brevicaule **Nutt. var.** ***pumilum*** **Stokes in Jones** Contr. W. Bot. 11: 10. 1903. Polygonaceae. = *E. brevicaule* var. *laxifolium* (T. & G.) Reveal Carbon Co., between Colton and Kyune, Jones 5603, 1894 (POM?).

Eriogonum cernuum **Nutt. var.** ***tenue*** **T. & G.** Proc. Amer. Acad. 8: 182. 1870. Polygonaceae. = *E. cernuum* var. *cernuum* Weber Co., Weber Valley, Watson 1036, 1869 (US!).

Eriogonum cernuum **Nutt. var.** ***umbraticum*** **Eastw.** Proc. Calif. Acad. II, 6:: 319. 1896. Polygonaceae. = *E. cernuum* var. *cernuum* San Juan Co., McElmo Creek, Eastwood sn, 1892 (CAS?).

Eriogonum chrysocephalum Gray ssp. ***alpestre*** Stokes Genus Eriogonum 93. 1936. Polygonaceae. = *E. panguicense* var. *alpestre* (Stokes) Reveal Iron Co., Cedar Breaks, Goodman & Hitchcock 1601, 1930 (CAS!; NY!;UTC!).

Eriogonum clavellatum Small Bull. Torrey Bot. Club 25: 48. 1898. Polygonaceae. San Juan Co., Bartons range, Eastwood 132, 1895 (US!;NY!).

Eriogonum confertiflorum var. ***stansburyi*** **Benth. in** DC Prodr. 14: 17. 1856. Polygonaceae. = *E. brevicaule* var. *brevicaule* Utah (label data illegible), Stansbury sn, 1850 (NY!).

Eriogonum corymbosum **Benth. in DC. var.** ***albogilvum*** Reveal Great Basin Naturalist 27: 218. 1967. Polygonaceae. = *E. x duchesnense* Reveal Duchesne Co., Indian Canyon, J & C Reveal 726, 1967 (US!;BRY!; NY!;UTC!).

Eriogonum corymbosum **Benth. in DC. var.** ***davidsei*** Reveal Great Basin Naturalist 27: 216. 1967. Polygonaceae. Carbon Co., Wellington, Reveal & Davidse 956, 1967 (US!;BRY!;UT!;RM!;NY!;UTC!;ISC!).

Eriogonum corymbosum **Benth. in DC. var.** ***divaricatum*** **T. & G. in** Beckwith Rep. U.S. Explor. & Surv. R.R. Pacific 2: 29. 1857. Polygonaceae. Emery Co., Green River, Creutzfeldt sn, 1853 (NY!).

Eriogonum corymbosum **Benth. in DC. var.** ***erectum*** **Reveal & Brotherson in** Reveal Great Basin Naturalist 27: 213. 1968. Polygonaceae. Wasatch Co., W Duchesne, Holmgren & Reveal 3022, 1966 (UTC!;US!; BRY!;UT!;NY!;ISC!).

Eriogonum corymbosum **Benth. in DC. var.** ***matthewsiae*** Reveal Phytologia 35: 441. 1976. Polygonaceae. Washington Co., Springdale, Welsh et al. 9509, 1969 (BRY!;UT!).

Eriogonum crispum **L.O. Williams** Bull. Torrey Bot. Club 59: 427. 1932. Polygonaceae. = *E. corymbosum* var. *glutinosum* (Jones) Jones Iron Co., Cedar Canyon, Garrett 6027, 1931 (RM!;UT!).

Eriogonum cronquistii Reveal Madroño 19: 289. 1969. Polygonaceae. Garfield Co., Henry Mts., Holmgren & Reveal 3010, 1966 (BRY!;RM!;UT!;NY!;US!;UTC!;ISC!).

Eriogonum deflexum **Torr. in Ives ssp.** ***hookeri*** **var.** ***gilvum*** Stokes Genus Eriogonum 45. 1936. Polygonaceae. = *E. hookeri* Wats. Davis Co., Antelope Island, Cottam 6407, 1935 (UT!;UTC!).

Eriogonum deflexum **Torr. in Ives ssp.** ***ultrum*** Stokes Genus Eriogonum 45. 1936. Polygonaceae. = *E. nutans* var. *nutans* Sevier Co., Sevier Valley, Eastwood & Howell 623, 1933 (CAS!).

Eriogonum duchesnense Reveal (hybrid) Great Basin Naturalist 27: 194. 1968. Polygonaceae. Syn: *E. corymbosum* var. *albogilvum* Reveal Duchesne Co., Indian Canyon, Reveal 678, 1964 (UTC;US!;BRY!;NY!;UTC!).

Eriogonum dudleyanum Stokes Genus Eriogonum 90. 1936. Polygonaceae. = *E. kearneyi* Tidestr. var. *kearneyi* Tooele Co., Skull Valley, Jones sn, 1896 (CAS!;UT!).

Eriogonum effusum Nutt. var. ***durum*** Stokes Genus Eriogonum 80. 1936. Polygonaceae. = *E. corymbosum* var. *corymbosum* Carbon Co., Sunnyside, Jones 1113a, 1901 (POM!;NY!).

Eriogonum effusum Nutt. ssp. ***orbiculatum*** Stokes Genus Eriogonum 79. 1936. Polygonaceae. = *E. corymbosum* var. *orbiculatum* (Stokes) Reveal & Brotherson Emery Co., Green River, Jones sn, 1915 (POM!;BRY!).

Eriogonum effusum Nutt. ssp. ***pallidum*** var. ***shandsii*** Stokes Genus Eriogonum 81. 1936. Polygonaceae. = *E. leptocladon* var. *leptocladon* San Juan Co., 3 mi s Indian Creek, Shands 130, 1931 (UT!).

Eriogonum ephedroides Reveal Madroño 19: 295. 1969. Polygonaceae. Uintah Co., 10 mi s Bonanza, Holmgren et al. 2265, 1965 (UTC!;BRY!;UT!;RM!;ISC!).

Eriogonum eremicum Reveal Phytologia 23: 165. 1972. Polygonaceae. Millard Co., se Garrison, Holmgren et al. 2247, 1965 (UTC!;BRY!;UT!;RM!;ISC!).

Eriogonum filicaule Stokes Genus Eriogonum 32. 1936. Polygonaceae. = *E. subreniforme* Reveal Washington Co., Springdale, Eastwood & Howell 1171, 1933 (CAS!;US!;NY!).

Eriogonum filiforme **L.O. Williams** Bull. Torrey Bot. Club 59: 428. 1932. Polygonaceae. = *E. wetherillii* Eastw. Wayne Co., w Hanksville, Garrett 5975, 1931 (UT!;RM!).

Eriogonum flexum Jones var. ***ferronis*** Jones Contr. W. Bot. 11: 15. 1903. Polygonaceae. = *E. flexum* Jones Emery Co., w Ferron, Jones 5454, 1894 (US!;POM!).

Eriogonum friscanum Jones Contr. W. Bot. 11: 14. 1903. Polygonaceae. = *E. microthecum* var. *foliosum* (T. & G.) Reveal Beaver Co., Frisco, Jones (POM?).

Eriogonum grayii Reveal Phytologia 25: 193. 1973. Polygonaceae. Salt Lake Co., Lake Blanche, Holmgren et al. 7121, 1947 (UTC!;BRY!;ISC!).

Eriogonum heracleoides Nutt. var. ***utahense*** **Gandg.** Bull. Soc. Bot. Belgium 42: 190. 1906. Polygonaceae. = *E. heracleoides* Nutt. var. *heracleoides* Cache Co., Linford sn, 1897 (US!).

Eriogonum hookeri Wats. Proc. Amer. Acad. 14: 295. 1879. Polygonaceae. Syn: *E. deflexum* ssp. *hookeri* var. *gilvum* Stokes Utah Co., American Fork Canyon, Watson 1033, 1869 (US!;NY!).

Eriogonum howellianum Reveal Phytologia 25: 204. 1973. Polygonaceae. Syn: *E. glandulosum* authors, not (Nutt.) Nutt. Millard Co, se Garrison, Holmgren et al 2248, 1965 (US!;BRY!;UT!;RM!;UTC!).

Eriogonum humivagans Reveal Madroño 19: 219. 1969. Polygonaceae. San Juan Co., 13.5 miles e Monticello, Holmgren & Reveal 3001, 1969 (UTC!; US!;RM!;BRY!;UT!;NY!;ISC!).

Eriogonum hylophilum **Reveal & Brotherson** Great Basin Naturalist 27: 190. 1968. Polygonaceae. Duchesne Co, Gate Canyon, Holmgren & Reveal 3017, 1966 (UTC!;US!;RM!;BRY!;UT!;NY!;ISC!).

Eriogonum insigne Wats. Proc. Amer. Acad. 14: 295. 1879. Polygonaceae. Iron Co., Red Creek, Palmer 431, 1877 (NY!;BRY!;ISC!).

Eriogonum intermontanum Reveal Madroño 19: 293. 1969. Polygonaceae. Grand Co., Middle Canyon, Roan Cliffs, Holmgren et al. 2278, 1965 (UTC!;BRY!; UT!;RM!;ISC!).

Eriogonum jamesii **Benth in DC. var.** ***rupicola*** **Reveal** Phytologia 25: 202. 1973. Polygonaceae. Washington Co., Zion National Park, Reveal & Reveal 2874, 1972 (US!;BRY!;NY!;UTC!).

Eriogonum kearneyi Tidestr. Proc. Biol. Soc. Washington 26: 122. 1913. Polygonaceae. Syn: *E. dudleyanum* Stokes Tooele Co., w Tooele, Kearney & Shantz 3218 (US!).

Eriogonum kingii var. ***laxifolium*** T. & G. Proc. Amer. Acad. 8: 165. 1870. Polygonaceae. = *E. brevicaule* Nutt. var. *laxifolium* (T. & G.) Reveal Salt Lake Co., Parleys Peak, Watson 1021, 1869 (US!).

Eriogonum lancifolium Reveal & Brotherson in Reveal Great Basin Naturalist 27: 188. 1967. Polygonaceae. Carbon Co., e Wellington, Reveal & Davidse 955, 1967 (UTC!;US!;RM!;BRY!;UT!;NY!;ISC!).

Eriogonum leptocladon T. & G. in Beckwith var. ***leptocladon*** Rep. U.S. Explor. & Surv. R.R. Pacific 2: 129. 1857. Polygonaceae. Syn: *E. effusum* spp. *pallidum* var. *shandsii* Stokes Emery Co., Green River, Creuzfeldt sn, 1853 (NY!).

Eriogonum loganum A. Nels. Bot. Gaz. 54: 149. 1912. Polygonaceae. Cache Co., Logan, Smith 1704, 1909 (RM!;BRY!).

Eriogonum longilobum Jones Proc. Calif. Acad. II, 5: 720. 1895. Polygonaceae. = *E. shockleyi* var. *longilobum* (Jones) Reveal Carbon Co., near Price, Jones 5590, 1894 (POM!;US!).

Eriogonum medium Rydb. Fl. Rocky Mts. 220, 1061. 1917. Polygonaceae. = *E. brevicaule* Nutt. var. *laxifolium* (T. & G.) Reveal Juab or Utah Co., Mt. Nebo, Rydberg sn, 1905 (US!;RM!;NY!).

Eriogonum nanum Reveal Phytologia 25: 194. 1973. Polygonaceae. Box Elder Co., Willard Peak, Reveal & Holmgren 665, 1964 (UT!;BRY!;RM!).

Eriogonum natum Reveal in Welsh, Atwood, & Reveal Great Basin Naturalist 35: 363. 1975. Polygonaceae. Millard Co, 43 mi w Delta, Reveal & Reveal 3924, 1975 (BRY!;NY!;UTC!).

Eriogonum nelsonii L.O. Williams Bull. Torrey Bot. Club 59: 428. 1937. Polygonaceae. = *E. microthecum* Nutt. var. *foliosum* (Torr.) Reveal San Juan Co., Geyser Basin, Walker 368, 1912 (RM!;UT!).

Eriogonum nudicaule Small ssp. ***garrettii*** Stokes Genus Eriogonum 83. 1936. Polygonaceae. = *E. brevicaule* Nutt. var. *brevicaule* Summit Co., Echo Reservoir, Garrett 7068, 1935 (US!;UT!;UTC!).

Eriogonum nudicaule Small ssp. ***ochroflorum*** Stokes Genus Eriogonum 83. 1936. Polygonaceae. = *E. spathulatum* Gray Sevier Co., Clear Creek Canyon, Jones 6104, 1894 (POM!;BRY!).

Eriogonum nudicaule Small ssp. ***parleyense*** Stokes Genus Eriogonum 84. 1936. Polygonaceae. = *E. brevicaule* Nutt. var. *brevicaule* Salt Lake Co., Parleys Canyon, Stokes 213, 1934 (CAS!;NY!;UTC!;BRY!).

Eriogonum nummulare Jones Contr. W. Bot. 11: 13. 1903. Polygonaceae. Tooele Co., Dutch Mt., Jones sn (POM?).

Eriogonum ochrocephalum var. ***angustum*** Jones Contr. W. Bot. 11: 9. 1903. Polygonaceae. = *E. brevicaule* Nutt. var. *laxifolium* (T. & G.) Reveal Tooele Co., Johnsons Pass, Jones sn (POM?).

Eriogonum ostlundii Jones Contr. W. Bot. 11: 12. 1903. Polygonaceae. Sevier Co., near Elsinore, Jones sn (POM?).

Eriogonum ovalifolium Nutt. var. ***utahense*** Gandg. Bull. Soc. Bot. Belgium 42: 191. 1906. Polygonaceae. = *E. ovalifolium* Nutt. var. *ovalifolium* Cache Co., Linford sn, 1897 (US!).

Eriogonum palmeri Wats. Proc. Amer. Acad. 14: 267. 1879. Polygonaceae. = *E. plumatella* Dur. & Hilg. Washington (?) Co., Palmer sn, 1870 (US!).

Eriogonum parryi Gray Proc. Amer. Acad. 10: 77. 1874. Polygonaceae. = *E. brachypodum* T. & G. Washington Co., St. George, Parry 239, 1874 (US!;NY!;BRY!).

Eriogonum pauciflorum var. ***panguicense*** Jones Contr. W. Bot. 11: 9. 1903. Polygonaceae. = *E. panguicense* (Jones) Reveal Garfield Co., Panguitch, Jones sn, 1890 (POM!).

Eriogonum pharnaceoides Torr. in Sitgr. var. ***cervinum*** Reveal Great Basin Naturalist 34: 245. 1974. Polygonaceae. Washington Co., Pine Valley Mts., Atwood & Higgins 5895, 1973 (US!;BRY!;RM!;UTC!).

Eriogonum porteri Small Bull. Torrey Bot. Club 25: 41. 1898. Polygonaceae. = *E. umbellatum* Torr. var. *porteri* (Small) Stokes Summit Co., Bear River Canyon, Watson 1014, 1869 (US!;NY!).

Eriogonum puberulum Wats. Proc. Amer. Acad. 14: 295. 1879. Polygonaceae. Iron Co., Red Creek, Palmer 429, 1877 (US!;NY!;BRY!;ISC!).

Eriogonum pulvinatum Small Bull. Torrey Bot. Club 25: 44. 1898. Polygonaceae. = *E. shockleyi* Wats. var. *shockleyi* Beaver Co., Milford, Jones 1775, 1880 (US!;UT!;POM!;NY!;UTC!).

Eriogonum ramosissimum Eastw. Proc. Calif. Acad. II, 6: 322. 1896. Polygonaceae. = *E. leptocladon* T. & G. var. *ramosissimum* (Eastw.) Reveal San Juan Co., Butter Spring, Eastwood 134, 1895 (US!;CAS!).

Eriogonum revealianum Welsh Great Basin Naturalist 30: 17. 1970. Polygonaceae. = *E. corymbosum* var. *revealianum* (Welsh) Reveal Garfield Co., s Antimony, Welsh & Welsh 9389, 1969 (BRY!;US!;UT!;RM!;NY!).

Eriogonum rubiflorum Jones Zoe 4: 281. 1893. Polygonaceae. = *E. nutans* T. & G. var. *nutans* Tooele Co., Dugway, Jones sn, 1891 (POM!;US!;NY!).

Eriogonum saurinum Reveal Great Basin Naturalist 27: 197. 1967. Polygonaceae. Uintah Co., 10 mi e Vernal, Holmgren & Reveal 3019, 1966 (UTC!;UT!;BRY!;US!;RM!;NY!;ISC!).

Eriogonum scabrellum Reveal Ann. Missouri Bot. Gard. 55: 74. 1968. Polygonaceae. Grand Co, Westwater, Reveal & Davidse 949, 1967 (UTC!;US!;BRY!;UT!;RM!;NY!;ISC!).

Eriogonum smithii Reveal Great Basin Naturalist 24: 202. 1967. Polygonaceae. Emery Co., San Rafael Desert, Holmgren & Reveal 3012, 1966 (UTC!;US!;BRY!;UT!;RM!;ISC!).

Eriogonum soredium Reveal Great Basin Nat. 41: 229. 1981. Polygonaceae. Beaver Co., Grampian Hill, near Frisco, Welsh et al. 20192,1980 (BRY!).

Eriogonum spathuliforme Rydb. Bull. Torrey Bot. Club 39: 307. 1912. Polygonaceae. = *E. ostlundii* Jones Piute Co., near Mt.Belknap, Stokes sn, 1900 (US!).

Eriogonum spathulatum Gray Proc. Amer. Acad. 10: 76. 1874. Polygonaceae. Syn: *E. nudicaule* Small ssp. *ochroflorum* Stokes Sevier (?) Co., Sevier River Valley, Parry 245, 1874 (ISC!).

Eriogonum subreniforme Wats. Proc. Amer. Acad. 12: 260. 1877. Polygonaceae. Syn: *E. filicaule* Stokes Washington Co., Parry 237, 1874 (ISC!).

Eriogonum sulcatum Wats. Proc. Amer. Acad. 14: 296. 1879. Polygonaceae. = *E. heermanii* var. *sulcatum* (Wats.) Munz & Reveal Washington Co., near St. George, Palmer 432, 1877 (US!;NY!;BRY!).

Eriogonum sulcatum Wats. var. ***argense*** Jones Contr. W. Bot. 11: 15. 1903. Polygonaceae. = *E. heermannii* Dur. & Hilg. var. *argense* (Jones) Munz Utah, Jones.

Eriogonum tenellum ssp. ***cottamii*** Stokes Genus Eriogonum 70. 1936. Polygonaceae. = *E. brevicaule* var. *cottamii* (Stokes) Reveal Utah Co., West Mountain, Cottam 411, 1925 (BRY!;UT!).

Eriogonum tenellum var. ***grandiflorum*** **Gandg.** Bull. Soc. Bot. Belgium 42: 197. 1906. Polygonaceae. = *E. microthecum* var. *laxiflorum* Hook. Rich Co., Linford sn, 1897 (?).

Eriogonum thompsonae Wats. var. ***albiflorum*** Reveal Madroño 19: 299. 1969. Polygonaceae. Washington Co., w Virgin, Holmgren & Reveal 2991, 1966 (UTC!; US!;BRY!;UT!;RM!;NY!;ISC!).

Eriogonum thompsonae Wats. var. ***thompsonae*** Amer. Naturalist 7: 302. 1873. Polygonaceae. Kane Co., Kanab, Thompson sn, 1872 (GH;US!;BRY!;NY!).

Eriogonum triste **Wats.** Proc. Amer. Acad. 10: 347. 1875. Polygonaceae. = *E. alatum* Torr. in Sitgr. Kane Co., Siler sn, 1873 (US!;NY!;BRY!;ISC!).

Eriogonum umbellatum **Torr.** var. ***desereticum*** **Reveal in Welsh, Atwood, & Reveal** Great Basin Naturalist 35: 365. 1975. Polygonaceae. Utah Co., Mt. Timpanogos, near Timpooneke Campground, Reveal 3702. 1974 (US!;BRY!;NY!;UTC!).

Eriogonum umbellatum **Torr.** var. ***glabratum*** Stokes Genus Eriogonum 109. 1936. Polygonaceae. = *E. umbellatum* Torr. var. *aureum* (Gandg.) Reveal Emery Co., Huntington Canyon, Garrett 7036, 1935 (UT!).

Eriogonum villiflorum Gray var. ***tumulosum*** Barneby Leafl. W. Bot. 5: 153. 1949. Polygonaceae. = *E. tumulosum* (Barneby) Reveal Emery Co., sw Woodside, Ripley & Barneby 8678, 1947 (CAS!;NY!;BRY!;UTC!).

Eriogonum viridulum Reveal Proc. Utah Acad. 42: 287. 1966. Polygonaceae. Duchesne Co., 8 mi e Duchesne, Reveal 675, 1964 (UTC!;BRY!;UT!;RM!;NY!;ISC!).

Eriogonum wasatchense Jones Contr. W. Bot. 11: 11. 1903. Polygonaceae. = *E. brevicaule* var. *wasatchense* (Jones) Reveal Utah Co., American Fork Canyon, Jones 1877, 1880 (US!;POM!;UTC!).

Eriogonum wetherillii **Eastw.** Proc. Calif. Acad. II, 6: 319. 1896. Polygonaceae. Syn: *E. filiforme* L.O. Williams San Juan Co., San Juan River, Eastwood 124, 1895 (CAS!).

Eriogonum zionis **J. T. Howell** Leafl. W. Bot. 2: 253. 1940. Polygonaceae. Washington Co, Zion National Park, Eastwood & Howell 6344, 1938 (CAS!).

Eritrichium barbigerum Gray Synop. Fl. N. Amer. 2(1): 194. 1878. Boraginaceae. = *Cryptantha barbigera* (Gray) Greene Washington Co., St. George, Parry 171, 1874 (GH;ISC!).

Eritrichium elongatum Wight var. ***paysonii*** **Johnst.** J. Arnold Arb. 33: 67. 1952. Boraginaceae. = *E. nanum* var. *elongatum* (Wight) Cronq. Summit Co., Uinta Mts, Maguire et al 14385, 1936 (RM!).

Eritrichium holopterum Gray Proc. Amer. Acad. 12: 81. 1876. Boraginaceae. = ? Southern Utah, Bishop sn, 1873 (GH?).

Eritrichium holopterum Gray var. ***submolle*** Gray Proc. Amer. Acad. 13: 374. 1878. Boraginaceae. = *Cryptantha utahensis* (Gray) Greene Washington Co., St. George, Palmer sn, 1870 (NY!).

Eritrichium pterocaryum Torr. var. ***pectinatum*** Gray Proc. Amer. Acad. 10: 61. 1874. Boraginaceae. = *Cryptantha pterocarya* var. *pterocarya* Southern Utah, Parry sn, 1874 (NY!).

Eritrichium setosissimum Gray Proc. Amer. Acad. 12: 80. 1876. Boraginaceae. = *Cryptantha setosissima* (Gray) Payson Sevier Co., Fish Lake, Ward sn, 1875 (GH).

Erysimum asperum **(Nutt.) DC.** var. ***purshii*** **Durand** Trans. Amer. Phil. Soc. II. 159. 1860. Brassicaceae. Syn: *E. capitatum* (Dougl.) Greene Salt Lake Co., near Great Salt Lake, Salt Lake Valley, Carrington sn, 1857 (P).

Erythrocoma brevifolia **Greene** Leafl. Bot. Obs. & Crit. 1: 176. 1906. Rosaceae. = *Geum triflorum* Pursh Garfield Co., Panguitch Lake, Jones 6002q, 1894 (US!).

Erythronium utahense **Rydb.** Fl. Rocky Mts. 165, 1061. 1917. Liliaceae. = *E. grandiflorum* Pursh Salt Lake Co., Salt Lake, Stansbury sn, 1850 (NY!).

Eschscholzia ludens **Greene** Pittonia 5: 272. 1905. Papaveraceae. = *E. minutiflora* Wats. Washington Co., St. George, Jones 5110a, 1894 (US!;POM!).

Euphorbia nephradenia **Barneby** Leafl. W. Bot. 10: 314. 1966. Euphorbiaceae. Kane Co., Cottonwood Canyon, Barneby 14434, 1966 (NY!;US!;BRY!;UTC!).

Euphorbia parryi **Engelm. in Parry** Amer. Naturalist 9: 350. 1875. Euphorbiaceae. Washington Co., near St. George, Parry s47, 1874 (MO).

Euphorbia podagrica **I.M. Johnston** Univ. Calif. Publ. Bot. 7: 440. 1922. Euphorbiaceae. Utah, Purpus 6432, 1898 (US!).

Euphorbia robusta **(Engelm.) Small ex Britt. & Brown** var. ***interioris*** **J.B.S. Norton** N. Amer. Euphorbia 49. 1899. Euphorbiaceae. = *E. robusta* (Engelm.) Small Wasatch Mts., Watson 1081, 1869 (US!).

Eurotia subspinosa **Rydb.** Bull. Torrey Bot. Club 39. 313. 1912. Chenopodiaceae. = *Ceratoides subspinosa* (Rydb.) J.T. Howell Washington Co., St. George, Goodding 810, 1903 (US!).

Festuca brevifolia **R. Br.** var. ***utahensis*** **St-Yves** Candollea 2: 257. 1925. Poaceae. = *F. ovina* L. Salt Lake Co., Alta, M.E.D. (possibly M.E.Jones) sn, 1895 (NY!).

Festuca dasyclada **Hack. ex Beal** Grasses N. Amer. 2: 602. 1896. Poaceae. Emery (?) Co., Parry 93, 1874 (US!;ISC!;NY!).

Festuca jonesii **Vasey** Contr. U.S. Natl. Herb. 1: 278. 1893. Poaceae. = *F. subulata* Trin. Salt Lake Co., City Creek Canyon, Jones sn, 1880 (US!;POM!).

Fragaria virginiana **Duchesne** var. ***glauca*** **Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 280. 1871. Rosaceae. = *F. virginiana* Duchesne Summit Co., Parleys Park, Watson 322, 1869 (US!;NY!).

Frasera albomarginata **Wats.** Rep. U.S. Geoi. Explor. 40th Parallel, Bot. 5: 220. 1871. Gentianaceae. = *Swertia albomarginata* (Wats.) Kuntze Washington Co., near St. George, Palmer, 1879 (US!;NY!).

Frasera utahensis **Jones** Zoe 2: 14. 1891. Gentianaceae. = *Swertia paniculata* (Torr.) St. John Kane (?) Co., (possibly House Rock Valley), Buckskin Mts., Jones sn, 1890 (US!;POM!).

Fraxinus anomala **Torr. in Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 283. 1871. Oleaceae. San Juan (?) Co., Labrynth Canyon, Newberry sn, 1859 (NY!).

Fritillaria dichroa **Gandg.** Bull. Soc. Bot. France 66: 291. 1920. Liliaceae. = *F. pudica* (Pursh) Spreng. Cache Co., Linford sn, 1897 (?).

***Fritillaria leucella* Gandg.** Bull. Soc. Bot. France 66: 291. 1920. Liliaceae. = *F. pudica* (Pursh) Spreng. Cache Co., Linford sn, 1897 (?).

***Fritillaria utahensis* Gandg.** Bull. Soc. Bot. France 66: 291. 1920. Liliaceae. = *F. pudica* (Pursh) Spreng. Cache Co., Linford sn, 1897 (?).

Gaillardia acaulis Gray Proc. Amer. Acad. 10: 73. 1874. Asteraceae. = *G. parryi* Greene Washington Co., St. George, Parry 120, 1874 (NY!;NDG!).

***Gaillardia crassifolia* Nels. & Macbr.** Bot. Gaz. 61: 46. 1916. Asteraceae. = *G. pinnatifida* Torr.? Washington Co., LaVerkin, Jones 5177, 1894 (US!;NY!;BRY!).

***Gaillardia flava* Rydb.** N. Amer. Fl. 34: 139. 1915. Asteraceae. Emery Co., Lower Crossing, Jones 6412, 1898 (US!;BRY!;POM!).

***Gaillardia gracilis* A. Nels.** Bot. Gaz. 37: 276. 1904. Asteraceae. = *G. pinnatifida* Torr. Washington Co., Diamond Valley, Goodding 894, 1902 (US!;RM!).

***Gaillardia spathulata* Gray** Proc. Amer. Acad. 12: 59. 1876. Asteraceae. Wayne Co., Rabbit Valley, Ward 401, 1875 (US!;NY!).

***Gaillardia straminea* A. Nels.** Univ. Wyoming Publ. Bot. 1: 137. 1926. Asteraceae. = *G. pinnatifida* Torr. Washington Co., LaVerkin, Jones 5177, 1894 (RM!;NY!;BRY!).

***Galium bifolium* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 134. 1871. Rubiaceae. Salt Lake Co. (?), Wasatch Mts., Watson 480, 1869 (US!;NY!).

***Galium desereticum* Dempst. & Ehrend.** Brittonia 17: 314. 1965. Rubiaceae. = *G. multiflorum* var. *multiflorum* Juab Co., Fish Springs, Jones sn, 1891 (US!;POM!).

***Galium filipes* Rydb.** Fl. Rocky Mts. 809, 1066. 1917. Rubiaceae. = *G. mexicanum* var. *asperulum* Gray Salt Lake Co., City Creek Canyon, Leonard 16665, 1883 (NY!).

***Galium hypotrichium* Gray ssp. *scabriusculum* Ehrend.** Contr. Dudley Herb. 5: 13. 1956. Rubiaceae. = *G. multiflorum* var. *multiflorum* Emery Co., Calf Spring Wash, Maguire 18437, 1940 (CAS!;UTC!).

***Galium hypotrichium* ssp. *utahense* Ehrend.** Contr. Dudley Herb. 5: 12. 1956. Rubiaceae. = *G. multiflorum* var. *multiflorum* Utah Co., Provo, Goodding 1116, 1902 (ISC!).

***Galium multiflorum* Kellogg var. *watsonii* Gray** Syn. Fl. N. Amer. 1(2): 40. 1884. Rubiaceae. = *G. multiflorum* var. *multiflorum* Syn: *G. watsonii* (Gray) Heller Wasatch Mts., Watson 484, 1869 (US!;NY!).

***Galium scabriusculum* (Ehrend.) Dempst. & Ehrend. ssp. *protoscabriusculum* Dempst. & Ehrend.** Brittonia 17: 312. 1965. Rubiaceae. = *G. multiflorum* var. *multiflorum* Carbon Co., Castle Gate, Ehrendorfer & Stutz 5954, 1959 (RM!;UTC!).

***Galium utahense* Eastw.** Leafl. W. Bot. 1: 55. 1933. Rubiaceae. = *G. boreale* L. Wasatch Co., Soldier Summit, Eastwood 7668, 1918 (CAS!).

Gentiana calycosa* Griseb. ssp. *apetala Maguire Madroño 6: 151. 1942. Gentianaceae. = *G. calycosa* Griseb. Duchesne Co., w Mt. Agassiz, Maguire et al. 4225, 1933 (UTC!).

***Gentiana tortuosa* Jones** Proc. Calif. Acad. II, 5: 707. 1895. Gentianaceae. = *Gentianella tortuosa* (Jones) Gillett Garfield Co., Panguitch Lake, Jones 6008, 1894 (POM!;US!).

***Geranium marginale* Rydb. ex Hanks & Small** N. Amer. Fl. 25: 16. 1907. Geraniaceae. Garfield Co., Aquarius Plateau, Rydberg & Carlton 7401, 1905 (NY!).

***Gilia aggregata* (Pursh) Spreng. ssp. *aggregata* var. *attenuata* f. *utahensis* Brand** Pflanzenreich 4. Fam. 250: 116. 1907. Polemoniaceae. = *G. aggregata* var. *macrosiphon* Kearney & Peebles Salt Lake Co., Alta, Jones 1122, 1879 (POM!;UTC!).

***Gilia arenaria* Benth. var. *rubella* Brand in Engler** Pflanzenreich 4. Fam. 250: 103. 1907. Polemoniaceae. = *G. hutchinsifolia* Rydb. Washington Co., St. George, Jones 1651, 1880 (US!;POM!;NY!).

***Gilia caespitosa* Gray** Proc. Amer. Acad 12: 80. 1876. Polemoniaceae. Wayne Co., Rabbit Valley, Ward 575, 1875 (US!;NY!;BRY!).

***Gilia congesta* Hook. var. *nuda* Eastw.** Proc. Calif. Acad. II, 6: 308. 1896. Polemoniaceae. = *G. roseata* Rydb. Syn: *G. nuda* (Eastw.) Rydb. San Juan Co., Willow Creek, Eastwood 80, 1895 (US!;CAS!).

***Gilia congesta* Hook. var. *paniculata* Jones** Proc. Calif. Acad. II, 5: 712. 1895. Polemoniaceae. = *G. congesta* var. *congesta* Emery Co., Huntington, Jones 5464m, 1894 (POM!;US!).

***Gilia debilis* Wats.** Amer. Naturalist 7: 302. 1873. Polemoniaceae. = *Collomia debilis* (Wats.) Greene Salt Lake Co., Wasatch Mts., above Salt Lake City, Wheeler sn, 1872 (US!).

***Gilia depressa* Jones in Gray** Proc. Amer. Acad. 16: 106. 1880. Polemoniaceae. Syn: *Ipomopsis depressa* (Jones) V. Grant Millard Co., Deseret, Jones 1772, 1880 (GH;US!;CAS!;POM!;BRY!;NY!;UTC!).

***Gilia filiformis* Parry ex Gray** Proc. Amer. Acad. 10: 75. 1874. Polemoniaceae. Washington Co., near St. George, Parry 187, 1874 (NY!;ISC!;BRY!).

***Gilia floribunda* var. *arida* Jones** Proc. Calif. Acad. II, 5: 713. 1895. Polemoniaceae. = *Leptodactylon watsonii* (Gray) Rydb. Wayne Co., Capitol Wash, Jones 5701a, 1894 (POM!;US!).

***Gilia frutescens* Rydb.** Bull. Torrey Bot. Club 40: 471. 1913. Polemoniaceae. = *G. congesta* var. *frutescens* (Rydb.) Cronq. Washington Co., Springdale, Jones 5247, 1894 (NY!;US!).

***Gilia gracilis* Hook. ssp. *spirillifera* var. *nana* Brand in Engler** Pflanzenr. 4. Fam. 250: 92. 1907. Polemoniaceae. = *Microsteris gracilis* (Hook.) Greene Millard Co., Fillmore, Jones 1684 (POM!;UT!).

***Gilia inconspicua* (J.E. Sm.) Sweet ssp. *euinconspicua* var. *variegata* Brand in Engler** Pflanzenr. 4. Fam. 250: 105. 1907. Polemoniaceae. = *G. inconspicua* (J.E. Sm.) Sweet Kane Co., Kanab, Jones 5280, 1894 (?).

***Gilia latifolia* Wats. in Parry** Amer. Naturalist 9: 347. 1875. Polemoniaceae. Washington Co., near St. George, Parry 188, 1874 (GH;US!;CAS!;NY!;BRY!;ISC!).

***Gilia leptomeria* Gray** Proc. Amer. Acad. 8: 278. 1870. Polemoniaceae. Syn: G. *leptomeria* var. *tridentata* Jones; G. triodon Eastw. Tooele Co., Stansbury Island, Watson 27, 1869 (NY!).

***Gilia leptomeria* Gray var. *tridentata* Jones** Proc. Calif. Acad. II, 5: 713. 1895. Polemoniaceae. = *G. leptomeria* Gray Emery Co., Emery, Jones 5445n, 1894 (POM;US!).

***Gilia mcvickerae* Jones** Proc. Calif. Acad. II, 5: 712. 1895. Polemoniaceae. = *G. pinnatifida* Nutt. Piute Co., Marysvale, Jones 5378, 1894 (POM!;US!;CAS!; BRY!;RM!;NY!).

***Gilia scopulorum* Jones** Bull. Torrey Bot. Club 8: 70. 1881. Polemoniaceae. Syn: *G. scopulorum* var. *deformis* Brand Washington Co., St. George, Jones 1659, 1880 (US!;POM!;NY!;UTC!).

***Gilia scopulorum* Jones var. *deformis* Brand** Pflanzenr. 4. Fam. 250: 109. 1907. Polemoniaceae. = *G. scopulorum* Jones? Southern Utah, Parry 198, 1874 (?).

***Gilia stenothrysa* Gray** Proc. Amer. Acad. 8: 276. 1870. Polemoniaceae. Duchesne (?) Co.,"Among cedars between Duchesne and Lake Fork," Fremont sn, 1845 (NY!).

***Gilia straminea* Rydb.** Bull. Torrey Bot. Club 40: 472. 1913. Polemoniaceae. = *G. inconspicua* var. *sinuata* (Hook.) Gray Washington Co., St. George, Palmer 325, 1877 (NY!).

***Gilia superba* Eastw.** Zoe 4: 123. 1893. Polemoniaceae. = *G. subnuda* Torr. San Juan Co., Hatches Wash, Eastwood sn, 1892 (CAS!;POM!).

***Gilia tenerrima* Gray** Proc. Amer. Acad. 8: 277. 1870. Polemoniaceae. Summit Co., Bear River Valley, Watson 922, 1869 (NY!).

***Gilia tenuituba* Rydb.** Bull. Torrey Bot. Club 40: 472. 1913. Polemoniaceae. = *G. aggregata* var. *macrosiphon* Kearney & Peebles Beaver (?) Co., Beaver City, Palmer 320, 1877 (NY!;US!).

***Gilia tridactyla* Rydb.** Fl. Rocky Mts. 692,1065. 1917. Polemoniaceae. Piute Co., Brigham Peak, Jones 5949, 1894 (US!;NY!;POM!).

***Gilia triodon* Eastw.** Zoe 4: 121. 1893. Polemoniaceae. = *G. leptomeria* Gray San Juan Co., Ruin Canyon, Eastwood sn, 1892 (CAS!).

***Gilia watsonii* Gray** Proc. Amer. Acad. 8: 267. 1870. Polemoniaceae. = *Leptodactylon watsonii* (Gray) Rydb. Salt Lake Co., Cottonwood Canyon, Watson sn, 1869 (NY!).

***Glycosma maxima* Rydb.** Bull. Torrey Bot. Club 40: 67. 1913. Apiaceae. = *Osmorhiza occidentalis* (Nutt.) Torr. Juab Co., Mt. Nebo, Rydberg & Carlton 7585, 1905 (NY!).

***Glyptopleura setulosa* Gray** Proc. Amer. Acad. 9: 211. 1874. Asteraceae. Washington Co., St. George, Palmer 6, 1870 (US!;NY!;BRY!).

***Grayia brandegei* Gray** Proc. Amer. Acad. 11: 101. 1876. Chenopodiaceae. San Juan (?) Co., San Juan R., Brandegee sn, 1875 (GH).

***Grindelia laciniata* Rydb.** Fl. Rocky Mts. 848, 1066. 1917. Asteraceae. = *G. fastigiata* Greene San Juan Co., Montezuma Canyon, Rydberg & Garrett 9692, 1911(NY!;US!).

***Grindelia stylosa* Eastw.** Proc. Calif. Acad. II, 6: 293. 1896. Asteraceae. = *Vanclevea stylosa* (Eastw.) Greene San Juan Co., Bartons range, Eastwood 713, 1895 (US!;CAS!;NY!).

***Gutierrezia sarothrae* (Pursh) Britt. & Rusby var. *pomariensis* Welsh** Great Basin Naturalist 30: 19. 1970. Asteraceae. = *Xanthocephalum sarothrae* var. *pomariense* (Welsh) Welsh Uintah Co., Orchard Creek Draw, Welsh etal. 9471, 1969 (BRY!).

***Gymnolomia hispida* Robins. & Greenm. var. *ciliata* Robins. & Greenm.** Proc. Boston Soc. Nat. Hist. 29: 93. 1899. Asteraceae. = *Heliomeris hispida* (Gray) Cockerell Syn: *Viguiera ciliata* (Robins. & Greenm.) Blake Southern Utah, Palmer 245, 1877 (US!).

***Gymnolomia linearis* Rydb.** Bull. Torrey Bot. Club 37: 327. 1910. Asteraceae. = *Heliomeris multiflora* var. *nevadensis* (A. Nels.) Yates Washington Co., St. George, Palmer 241, 1877 (NY).

***Gymnolomia multiflora* var. *annua* Jones** Proc. Calif. Acad. II, 5: 698. 1895. Asteraceae. = *Heliomeris longifolia* var. *annua* (Jones) Yates Utah?, Jones ?, (?).

***Hackelia ibapensis* Shultz & Shultz** Brittonia 33: 157. 1981. Boraginaceae. Juab Co., Deep Creek Range, L. & J. Shultz 4350, 1980 (NY!;UTC!).

***Hackelia patens* (Nutt.) Johnst. var. *harrisonii* Gentry** Southw. Naturalist 19: 140. 1974. Boraginaceae. Washington Co., Pine Valley, Gentry 2002, 1968 (NY!; CAS!;BRY!;UTC!).

***Halostachys occidentalis*| Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 293. 1871. Chenopodiaceae. = *Allenrolfia occidentalis* (Wats.) Kuntze Box Elder Co., Raft River Valley, Watson 995, 1869 (US!).

***Hamosa atratiformis* Rydb.** Bull. Torrey Bot. Club 34: 48. 1907. Fabaceae. = *Astragalus straturensis* Jones Wahington Co., Parry 47, 1874 (NY!;ISC!).

***Haplopappus cervinus* Wats.** Amer. Naturalist 7: 301. 1873. Asteraceae. Utah, Antelope Canyon, Wheeler sn, 1872 (US!).

***Haplopappus nuttallii* T. & G. var. *depressus* Maguire** Amer. Midl. Naturalist 37: 144. 1947. Asteraceae. = *M. grindelioides* var. *depressa* (Maguire) Cronq. & Keck Millard Co., Desert Experimental Range, Maguire 20859, 1941 (US!;NY!;UTC!).

***Haplopappus parryi* Gray var. *minor* Gray** Syn. Fl. N. Amer. 1(2): 131. 1884. Asteraceae. = *Solidago parryi* (Gray) Greene Salt Lake Co., Alta, Bald Mtn., Jones sn?, 1879 (POM!;BRY!;NDG!).

***Haplopappus scopulorum* (Jones) Blake in Tidestr. var. *hirtellus* Blake** Proc. Biol. Soc. Washington 48: 170. 1935. Asteraceae. Iron Co., Cedar Canyon, Garrett 6051, 1931 (US!;UT!).

***Hedysarum gremiale* Rollins** Rhodora 42: 230. 1940. Fabaceae. = *H. boreale* var. *gremiale* (Rollins) Northstrom & Welsh Uintah Co., 14 mi n Vernal, Rollins 1733, 1937 (US!;CAS!;RM!;UTC!).

***Hedysarum occidentale* Greene var. *canone* Welsh** Great Basin Naturalist 38: 314. 1978. Fabaceae. Carbon Co., Soldier Creek, Welsh & Taylor,15256, 1977 (BRY!;NY!).

***Hedysarum utahense* Rydb.** Bull. Torrey Bot. Club 34: 425. 1907. Fabaceae. = *H. boreale* var. *boreale* Salt Lake Co., Salt Lake City, Leonard 55, 1883 (NY!).

***Helianthella multicaulis* D.C. Eaton in Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 170. 1871. Asteraceae. = *H. uniflora* (Nutt.) T. & G. Summit Co., Parleys Park, Watson 605, 1869 (US!;NY!).

***Helianthus anomalus* Blake** J. Washington Acad. Sci. 21: 333. 1931. Asteraceae. Wayne Co., s Hanksville, Stanton 4806, 1930 (US!;UT!).

***Helianthus bracteatus* E.E. Watson** Papers Michigan Acad. Sci. 9: 393. 1929. Asteraceae. = *H. nuttallii* T. & G. Cache Co., Logan, Mulford 177, 1898 (MO).

Helianthus deserticolus Heiser Proc. Indiana Acad. Sci. 70: 209. 1961. Asteraceae. Washington Co., w Hurricane, Stoutamire 2574, 1957 (IND).

***Helianthus giganteus* var. *utahensis* D.C. Eaton** in Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 169. 1871. Asteraceae. = *H. nuttallii* T. & G. Wasatch Mts., Watson 603, 1869 (US!).

***Hermidium alipes* Wats. var. *pallidum* C.L. Porter** Rhodora 54: 158. 1952. Nyctaginaceae. = *Mirabilis alipes* (Wats.) Pilz Uintah Co., 5 mi sw Vernal, Porter 5308, 1950 (RM!;CAS!).

***Hesperanthes albomarginata* Jones** Zoe 2: 251. 1891. Liliaceae. = *Eremocrinum albomarginatum* (Jones) Jones Emery Co., Green River, Jones sn, 1890 (?).

***Heuchera rubescens* Torr.** in **Stansb.** Explor. Great Salt Lake 388. 1852. Saxifragaceae. Syn: *H. versicolor* Greene; *H. versicolor* f. *pumila* Rosend., Butters, & Lakela Davis (?) Co., Great Salt Lake, Stansbury sn, 1850 (NY!).

Heuchera utahensis Rydb. N. Amer. Fl. 22: 114. 1905. Saxifragaceae. = *H. parvifolia* Nutt. Salt Lake Co., City Creek Canyon, Jones 1458, 1880 (US!;CAS!; RM!;POM!;UT!;BRY!;UTC!).

***Heuchera versicolor* Greene f. *pumila* Rosend., Butters, & Lakela** Minnesota Studies Pl. Sci. 2: 85. 1936. Saxifragaceae. = *H. rubescens* Torr. Utah? (?).

***Hieracium utahense* Gandg.** Bull. Soc. Bot. France 65: 49. 1918. Asteraceae. = *H. gracile* Hook. Cache Co., Linford sn, 1897 (?).

***Holodiscus microphyllus* Rydb.** Bull. Torrey Bot. Club 31: 559. 1904. Rosaceae. = *H. dumosus* (Nutt.) Heller Salt Lake Co., Alta, Jones 1142, 1879 (POM!;BRY!;NY!;UTC!).

Homalobus canovirens Rydb. Fl. Rocky Mts. ed. 2. 1126. 1922. Fabaceae. = *Astragalus coltonii* var. *moabensis* Jones Grand Co., La Sal Mts, Rydberg & Garrett 8536, 1913 (NY!).

Homalobus humilis Rydb. Bull. Torrey Bot. Club 34: 417. 1907. Fabaceae. = *Astragalus miser* var. *oblongifolius* (Rydb.) Cronq. Piute Co., n Bullion Creek, Rydberg & Carlton 7147, 1905 (NY!;US!;RM!;BRY!).

Homalobus paucijugus Rydb. Bull. Torrey Bot. Club 34: 418. 1907. Fabaceae. = *Astragalus miser* var. *tenuifolius* (Nutt.) Barneby Syn: *A. garrettii* Macbr. Salt Lake Co., Big Cottonwood Canyon, Garrett 1580, 1905 (NY!;US!;UT!).

***Hordeum pusillum* Nutt. var. *pubens* A.S. Hitchc.** J. Washington Acad. Sci. 23: 453. 1933. Poaceae. = *H. pusillum* Nutt. Washington Co., LaVerkin, Jones 5196ro, 1894 (POM!).

***Hosackia rigida* Benth. var. *nummularia* Jones** Proc. Calif. Acad. 11, 5: 633. 1895. Fabaceae. = *Lotus longebracteatus* Rydb. Washington Co., Rockville, Jones 5224, 1894 (US!;RM!).

Houstonia saxicola Eastw. Proc. Calif. Acad. 11, 6: 291. 1896. Rubiaceae. = *H. rubra* Cav. San Juan Co., Butler Spring, Eastwood 33, 1895 (CAS!).

***Hymenopappus eriopodus* A. Nels.** Bot. Gaz. 37: 274. 1904. Asteraceae. = *H. filifolius* var. *eriopodus* (A. Nels.) Turner Washington Co., Diamond Valley, Goodding 880, 1902 (RM!;US!;NY!).

***Hymenopappus niveus* Rydb.** N. Amer. Fl. 34: 52. 1914. Asteraceae. = *H. filifolius* var. *tomentosus* (Rydb.) Turner Washington Co., Springdale, Jones 5261, 1894 (US!;NY!).

Hymenopappus nudipes Maguire Amer. Midl. Naturalist 37: 143. 1947. Asteraceae. = *H. filifolius* var. *alpestris* (Maguire) Shinners Kane Co., 15 mi n Orderville, Maguire 18740, 1940 (NY!;US!).

Hymenopappus nudipes Maguire **var. *alpestris*** Maguire Amer. Midl. Naturalist 37: 144. 1947. Asteraceae. = *H. filifolius* var. *alpestris* (Maguire) Shinners Iron Co., Cedar Breaks, Maguire 19023, 1940 (US!; NY!;UTC!).

***Hymenopappus pauciflorus* Johnst.** Contr. Gray Herb. 11, 68: 97. 1923. Asteraceae. = *H. filifolius* var. *pauciflorus* (Johnst.) Turner San Juan Co., near Bluff, Rydberg & Garrett 9951, 1911 (UT!;NY!).

Hymenopappus tomentosus Rydb. Bull. Torrey Bot. Club 27: 633. 1900. Asteraceae. = *H. filifolius* var. *tomentosus* (Rydb.) Turner Washington Co., St. George, Palmer 270, 1877 (NY!;ISC!;BRY!).

***Hymenoxys lemmonii* (Greene) Cockerell ssp. *greenei* Cockerell** Bull. Torrey Bot. Club 31: 479. 1904. Asteraceae. = *H. lemmonii* (Greene) Cockerell Washington (?) Co., Rock Creek, Palmer 261, 1877 (US!;NY!).

***Hymenoxys richardsonii* (Hook.) Cockerell var. utahensis** *Cockerell* Bull. Torrey Bot. Club 31: 477. 1904. Asteraceae. = *H. richardsonii* (Hook.) Cockerell Emery Co., Emery, Jones 5442, 1894 (US!;POM!).

***Ivesia utahensis* Wats.** Proc. Amer. Acad. 10: 71. 1874. Rosaceae. Salt Lake Co., Bald Mt., Jones 1231, 1879 (US!;NY!;UTC!)).

***Juncus canadensis* var. *kuntzei* Buch.** Bot. Jahrb. 12: 272. 1890. Juncaceae. = *J. tweedyi* Rydb. Box Elder Co., near Corinne, Kuntze 3133, 1874 (NY!).

***Juncus jonesii* Rydb.** Fl. Rocky Mts. 153, 1061. 1917. Juncaceae. = *J. regelii* Buch. Salt Lake Co., Alta, Jones 119, 1879 (NY!;POM!).

***Juncus tracyi* Rydb.** Fl. Rocky Mts. 155, 1061. 1917. Juncaceae. = *J. ensifolius* Wikstr. Weber Co., Ogden, Tracy 389, 1887 (US!;NY!).

Juncus utahensis Martin Rhodora 40: 69. 1938. Juncaceae. = *J. ensifolius* var. *brunnescens* (Rydb.) Cronq. Summit (?) Co., Ashley National Forest, Nord & Sargent 1, 1927 (US!).

Juniperus californica* var. *utahensis Vasey Cat. Forest Trees U.S. 37. 1876. Cupressaceae. = *J. osteosperma* (Torr.) Little Wasatch Mts., Ward sn, 1875 (ISC!).

Juniperus californica* var. *utahensis Engelm. Trans. Acad. Sci. St. Louis 3: 588. 1878. Cupressaceae. = *J. osteosperma* (Torr.) Little Syn: *J. utahensis* (Engelm.) Lemmon Washington Co., St. George, Palmer? sn, 1877 (?).

***Kochia americana* Wats. var. *vestita* Wats.** Proc. Amer. Acad. 9: 93. 1874. Chenopodiaceae. = *K. americana* Wats. Tooele Co., "Tuilla Valley" Watson 991, 1869 (US!;NY!).

Krynitzkia echinoides Jones Proc. Calif. Acad. 11, 5: 709. 1895. Boraginaceae. = *Cryptantha fulvocanescens* var. *echinoides* (Jones) Higgins Garfield (?) Co., Pahria Canyon, Jones 5297p, 1894 (US!;POM!).

Krynitzkia glomerata* var. *acuta Jones Zoe 2: 250. 1891. Boraginaceae. = *Cryptantha wetherillii* (Eastw.) Payson Grand Co., Cisco, Jones sn, 1890 (?).

Krynitzkia glomerata* var. *virginensis Jones Contr. W. Bot. 13: 5. 1910. Boraginaceae. = *Cryptantha virginensis* (Jones) Payson Washington Co., LaVerkin, Jones 5195a, 1894 (US!;RM!;POM!).

Krynitzkia leucophaea var. ***alata*** **Jones** Proc. Calif. Acad. II, 5: 710. 1895. Boraginaceae. = *Cryptantha confertiflora* (Greene) Payson Kane Co., Johnson, Jones 5289f, 1894 (POM!;US!;BRY!;NY!).

Krynitzkia mensana **Jones** Contr. W. Bot. 13: 4. 1910. Boraginaceae. = *Cryptantha mensana* (Jones) Payson Emery Co., Emery, Jones 5445p, 1894 (POM!; US!;RM!).

Krynitzkia multicaulis var. ***setosa*** **Jones** Cotr. W. Bot. 13: 4. 1910. Boraginaceae. = *Cryptantha cinerea* (Greene) Cronq. Syn: *C. jamesii* var. *setosa* (Jones) Johnst. Millard Co., near Cove Fort, Jones sn, 1901 (POM!).

Krynitzkia utahensis **Gray** Syn Fl. N. Amer. ed.2. 2(1): 427. 1886. Boraginaceae. = *Cryptantha utahensis* (Gray) Greene Washington Co., St. George, Palmer 352, 1877 (US!).

Krynitzkia watsonii **Gray** Proc. Amer. Acad. 20: 271. 1885. Boraginaceae. = *Cryptantha watsonii* (Gray) Greene Wasatch Mts., Watson 858, 1869 (US!;NY!).

Langloisia setosissima **(T. & G.) Greene** var. ***campylocladas*** **Brand** Pflanzenreich 4. Fam. 250: 171. 1907. Polemoniaceae. = *L. setosissima* (T. & G.) Greene Washington Co., near St. George, Parry 190, 1874 (US!;ISC!).

Laphamia palmeri **Gray** Proc. Amer. Acad. 13: 372. 1878. Asteraceae. = *Perityle tenella* (Jones) Macbr. Washington Co., (Note: At Beaverdam in Ariz.) Palmer 199, 1877 (US!;NY!).

Laphamia palmeri **Gray** var. ***tenella*** **Jones** Proc. Calif. Acad. II, 5: 703. 1895. Asteraceae. = *Perityle tenella* (Jones) Macbr. Washington Co., Springdale, Jones 52491, 1894 (US!;POM!;NY!;BRY!).

Laphamia stansburyi **Gray** Pl. Wright. 1: 101. 1852. Asteraceae. = *Perityle stansburyi* (Gray) Macbr. Tooele Co., Stansbury Island, Stansbury sn, 1850 (NY!;BRY!).

Lappula collina **Greene** Pittonia 4: 96. 1899. Boraginaceae. = *L. occidentalis* (Wats.) Greene sens. lat. Piute Co., Kingston, Jones sn, 1894 (?).

Lathyrus brachycalyx **Rydb.** var. ***brachycalyx*** Bull. Torrey Bot. Club 34: 425. 1907. Fabaceae. Salt Lake Co., City Creek Canyon, Leonard 101, 1883 (NY!).

Lathyrus coriaceus **White** Bull. Torrey Bot. Club 21: 452. 1894. Fabaceae. = *L. lanzwertii* var. *lanzwertii* Wasatch Mts., Watson 297, 1869 (US!).

Lathyrus utahensis **Jones** Proc. Calif. Acad. II, 5: 678. 1895. Fabaceae. = *L. pauciflorus* var. *utahensis* (Jones) Peck Sevier Co., Irelands Ranch, Jones 54411, 1894 (US!;NY!).

Lathyrus zionis **C.L. Hitchc.** Univ. Washington Publ. Biol. 15: 36. 1952. Fabaceae. = *L. brachycalyx* var. *zionis* (C.L. Hitchc.) Welsh Kane Co., 10 mi e Zion N.P., Hitchcock 19013, 1949 (CAS!,RM!;UTC!;NY!).

Lepidium brachybotryum **Rydb.** Bull. Torrey Bot.club 34: 427. 1907. Brassicaceae. = *L. montanum* var. *montanum* Juab Co., Juab, Goodding 1075, 1902 (NY!;US!;RM!).

Lepidium georginum **Rydb.** Bull. Torrey Bot. Club 30: 253. 1903. Brassicaceae. = *L. lasiocarpum* var. *georginum* (Rydb.) C.L. Hitchc. Washington Co., Southern Utah, Parry 19, 1874 (NY!;ISC!).

Lepidium jonesii **Rydb.** Bull. Torrey Bot. Club 29: 233. 1902. Brassicaceae. = *L. montanum* var. *jonesii* (Rydb.) C.L. Hitchc. Washington Co., St. George, Jones 1636, 1880 (US!;CAS!;RM!;POM!;NY!).

Lepidium montanum **Nutt. in T. & G.** var. ***alpinum*** Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 29. 1871. Brassicaceae. Salt Lake Co., Cottonwood Canyon, Watson 122, 1869 (US!;NY!).

Lepidium montanum **Nutt. in T. & G.** var. ***demissum*** **C.L. Hitchc.** Madroño 10: 157. 1950. Brassicaceae. = *L. barnebyanum* Reveal Duchesne Co., sw Duchesne, Ripley & Barneby 8699, 1947 (US!;CAS!;NY!).

Lepidium montanum **Nutt. in T. & G.** var. ***neeseae*** **Welsh & Reveal** Great Basin Naturalist 34: 334. 1977. Brassicaceae. Garfield Co., Hells Backbone, Neese & White 3332, 1977 (BRY!;NY!;UT!).

Lepidium montanum **Nutt. in T. & G.** var. ***stellae*** **Welsh & Reveal** Great Basin Naturalist 34: 334. 1977. Brassicaceae. Kane Co., se Cannonville, Welsh & Welsh 12841, 1975 (BRY!).

Lepidium ostler **Welsh & Goodrich** Great Basin Naturalist 40: 80. 1980. Brassicaceae. Beaver Co., Frisco, Ostler & Anderson 1258, 1978 (BRY!).

Lepidium utahense **Jones** Zoe 4: 266. 1893. Brassicaceae. = *L. integrifolium* Nutt. Beaver Co., Milford, Jones 1821, 1880 (POM!;NY!;BRY!;UT!;UTC!;ISC!).

Lepidium zionis **A. Nels.** Bot. Gaz. 42: 50. 1906. Brassicaceae. = *L. integrifolium* Nutt. Sevier Co., Richfield, Jones 5411, 1894 (RM!;BRY!;POM!;NY!).

Leptodactylon brevifolium **Rydb.** Bull Torrey Bot. Club. 40: 474. 1913. Polemoniaceae. = *L. pungens* (Torr.) Nutt. Iron Co., Juniper Range, Purpus 6306, 1898 (US!).

Leptotaenia eatonii **Coult. & Rose** Rev. N. Amer. Umbell. 52. 1888. Apiaceae. = *Lomatium dissectum* var. *eatonii* (Coult. & Rose) Cronq. Utah, Eaton 147, 1869 (?).

Lesquerella garrettii **Payson** Ann. Missouri Bot. Gard. 8: 213. 1921. Brassicaceae. Salt Lake Co., Big Cottonwood Canyon, Garrett 1344, 1908 (MO!;RM!).

Lesquerella gordonii var. ***sessilis*** **Wats.** Proc. Amer. Acad. 23: 253. 1888. Brassicaceae. = *L. tenella* A. Nels. Washington Co., near St. George, Parry sn, 1874 (GH).

Lesquerella hemiphysaria **Maguire** var. ***hemiphysaria*** Amer. Midl. Naturalist 27: 456. 1942. Brassicaceae. Sanpete Co., Wasatch Plateau, Maguire 20053, 1940 (UTC!).

Lesquerella hemiphysaria **Maguire** var. ***lucens*** **Welsh & Reveal** Great Basin Naturalist 37: 338. 1977. Brassicaceae. Carbon Co., Range Creek, Welsh & Taylor 15139, 1977 (BRY!).

Lesquerella hitchcockii ssp. ***tumulosa*** **Barneby** Leafl. W. Bot. 10: 313. 1966. Brassicaceae. = *L. tumulosa* (Barneby) Reveal Kane Co., se Cannonville, Barneby 14424, 1966 (US!;BRY!;UTC!;NY!).

Lesquerella multiceps **Maguire** Amer. Midl. Naturalist 27: 465. 1942. Brassicaceae. Cache Co., Tony Grove Lake, Maguire 16030, 1938 (UTC!;RM!).

Lesquerella rubicundula **Rollins** Contr. Dudley Herb. 3: 178. 1941. Brassicaceae. Garfield Co., Red Canyon, Eggleston 8198, 1912 (US!).

Lesquerella subumbellata **Rollins** Rhodora 57: 255. 1955. Brassicaceae. Uintah Co., n Vernal, Rollins 175, 1937 (US!;RM!;NY!;UTC!).

Lesquerella utahensis **Rydb.** Bull. Torrey Bot. Club 30: 252. 1903. Brassicaceae. Utah Co., American Fork Canyon, Jones 1354, 1880 (NY!;US!;CAS!).

Lesquerella wardii **Wats.** Proc. Amer. Acad. 23: 252. 1888. Brassicaceae. Garfield Co., Aquarius Plateau, Ward 589, 1875 (GH;US!;RM!).

***Ligusticum brevilobum* Rydb.** Fl. Rocky Mts. 613, 1064. 1917. Apiaceae. = *L. porteri* Coult. & Rose Garfield Co., Aquarius Plateau, Rydberg & Carlton 7473, 1905 (NY!;US!).

***Ligusticum filicinum* Wats.** Proc. Amer. Acad. 11: 140. 1876. Apiaceae. Summit (?) Co., Uinta Mts., Watson 454, 1869 (US!;NY!).

***Limnia utahensis* Rydb.** Bull. Torrey Bot. Club 39: 314. 1912. Portulacaceae. = *Montia perfoliata* (Donn) Howell Washington Co., St. George, Palmer 56, 1877 (NY!).

***Linosyris serrulata* Torr. in Stansb.** Explor. Great Salt Lake 389. 1852. Asteraceae. = *Chrysothamnus viscidiflorus* var. *viscidiflorus* Salt Lake Co., Salt Lake Valley, Stansbury sn, 1850 (NY!).

***Linum aristatum* Engelm. in Wisliz. var. *subteres* Trel. in Eastwood** Proc. Calif. Acad. II, 6: 285. 1896. Linaceae. = *L. subteres* (Trel.) Winkler San Juan Co., Willow Creek, Eastwood sn, 1895 (?).

***Linum kingii* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 49. 1871. Linaceae. Summit Co., Uintas, Watson 203, 1869 (US!).

***Linum kingii* Wats. var. *pinetorum* Jones** Proc. Calif. Acad. II, 5: 628. 1895. Linaceae. = *L. kingii* Wats. Garfield Co., canyon above Tropic, Jones 5306, 1894 (US!;POM!;NY!;BRY!).

***Lomatium jonesii* Coult. & Rose** Contr. U.S. Natl. Herb. 7: 233. 1900. Apiaceae. = *L. foeniculaceum* var. *macdougalii* (Coult. & Rose) Cronq. Sevier Co., Irelands Ranch, Jones 5435, 1894 (US!).

***Lomatium junceum* Barneby & Holmgren** Brittonia 31: 96. 1979. Apiaceae. Emery Co., San Rafael Swell, Holmgren et al. 8778, 1978 (NY!;BRY!;UTC!).

***Lonicera utahensis* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 133. 1871. Caprifoliaceae. Salt Lake Co., Cottonwood Canyon, Watson 477, 1869 (US!;NY!).

***Lotus longebracteatus* Rydb.** Bull. Torrey Bot. Club 30: 254. 1903. Fabaceae. Syn: *L. oroboides* var. *nummularius* (Jones) Isely Washington Co., "South Utah" ("Mokaik Pass"), Palmer 94, 1877 (US!;NY!;BRY!).

***Lotus utahensis* Ottley** Brittonia 5: 108. 1944. Fabaceae. Kane Co., w Carmel, Ferguson & Ottley 5613 (?).

***Lupinus aegra-ovium* C.P. Sm.** Sp. Lupinorum 694. 1951. Fabaceae. = *L. sericeus* var. *sericeus* sens. lat. Sevier Co., Salina Experiment Station, Huffman 49–9, 1949 (CAS!).

***Lupinus aridus* var. *utahensis* Wats.** Proc. Amer. Acad. 8: 534. 1873. Fabaceae. = *L. caespitosus* Nutt.; Syn: *L. watsonii* Heller Summit Co., Parleys Park, Watson 234, 1869 (US!).

***Lupinus barbiger* Wats.** Proc. Amer. Acad. 8: 528. 1873. Fabaceae. = *L. sericeus* var. *barbiger* (Wats.) Welsh Kane Co., S. Utah, Siler sn, 1872? (GH).

***Lupinus eatonanus* C.P. Sm.** Sp. Lupinorum 671. 1949. Fabaceae. = *L. leucophyllus* Dougl. Wasatch Co., Hailstone, Smith 3995, 1925 (CAS!).

***Lupinus garrettianus* C.P. Sm.** Sp. Lupinorum 672. 1949. Fabaceae. = *L. argenteus* var. *argenteus* Duchesne Co., 1 mi w Duchesne, Garrett 8303, 1940 (UT!).

***Lupinus holosericeus* var. *utahensis* Wats.** Proc. Amer. Acad. 8: 533. 1873. Fabaceae. = *L. caudatus* var. *caudatus* Salt Lake Co. ?, Watson sn?, 1869 (US!).

***Lupinus huffmanii* C.P. Sm.** Sp. Lupinorum 693. 1951. Fabaceae. = *L. sericeus* var. *sericeus* sens. lat. Sevier Co., Salina Experiment Station, Huffman 47–7A, 1949 (CAS!).

***Lupinus jonesii* Rydb.** Bull. Torrey Bot. Club 30: 256. 1903. Fabaceae. Syn: *L. leucanthus* Rydb. Washington Co., Silver Reef, Jones 5143, 1894 (US!;RM!;BRY!;NY!).

***Lupinus larsonanus* C.P. Sm.** Sp. Lupinorum 696. 1951. Fabaceae. = *L. sericeus* var. *sericeus* sens. lat. Sevier Co., inter Browns Hole & Hoodoo, Larson sn, 1934 (CAS!).

***Lupinus leucanthus* Rydb.** Bull. Torrey Bot. Club 30: 259. 1903. Fabaceae. = *L. jonesii* Rydb. Washington Co., Springdale, Jones 5249e, 1894 (US!;RM!; BRY!;POM!;NY!).

***Lupinus leucophyllus* Dougl. ex Lindl. var. *lupinus* Rydb.** Bull. Torrey Bot. Club 40: 44. 1913. Fabaceae. Syn: *L. utahensis* Moldenke = *L. caudatus* var. *caudatus* San Juan Co., Bears Ears, Rydberg & Garrett 9363, 1911 (NY!).

***Lupinus maculatus* Rydb.** Bull. Torrey Bot. Club 30: 257. 1903. Fabaceae. Utah Co., Pleasant Valley (P.V.) Jct., Jones sn, 1883 (NY!;US!;POM!;UTC!).

***Lupinus marianus* Rydb.** Bull. Torrey Bot. Club 34: 41. 1907. Fabaceae. = *L. sericeus* var. *marianus* (Rydb.) Welsh Piute Co., Bullion Creek, Rydberg & Carlon 7024, 1905 (US!;RM!;NY!).

***Lupinus prunophilus* Jones** Contr. W. Bot. 13: 7. 1910. Fabaceae. Juab Co., Robinson, Jones sn, 1909 (CAS!;POM!;BRY!;NY!).

***Lupinus pulcher* Eastw.** Leafl. W. Bot. 3: 173. 1942. Fabaceae. = *L. hillii* Greene Iron Co., 18 mi s Cedar City, Barkley & Reed 4069, 1939 (CAS!).

***Lupinus puroviridis* C.P. Sm.** Sp. Lupinorum 694. 1951. Fabaceae. = *L. sericeus* var. *sericeus* sens. lat. Sevier Co., Salina Experiment Station, Huffman 49–7B, 1949 (CAS!).

***Lupinus quercus-jugi* C.P. Sm.** Sp. Lupinorum 696. 1951. Fabaceae. = *L. sericeus* var. *sericeus* sens. lat. Sevier Co., Browns Hole, Clawson C241, 1935 (CAS!).

***Lupinus rickeri* C.P. Sm.** Sp. Lupinorum 695. 1951. Fabaceae. = *L. sericeus* var. *sericeus* sens. lat. Sevier Co., Salina Experiment Station, Ricker 14080, 1917 (CAS!).

***Lupinus rubens* Rydb.** Bull. Torrey Bot. Club 34: 45. 1907. Fabaceae. = *L. pusillus* var. *rubens* (Rydb.) Welsh Washington Co., St. George, Parry 41, 1874 (NY!;ISC!).

***Lupinus salinensis* C.P. Sm.** Sp. Lupinorum 695. 1951. Fabaceae. = *L. sericeus* var. *sericeus* sens. lat. Sevier Co., Salina Experiment Station, Clawson C.202, 1935 (CAS!).

***Lupinus sileri* Wats.** Proc. Amer. Acad. 10: 345. 1875. Fabaceae. = *L. kingii* Wats. Southern Utah, Siler sn (GH).

***Lupinus spatulatus* Rydb.** Bull. Torrey Bot. Club 29: 244. 1902. Fabaceae. = *L. argenteus* var. *boreus* (C.P. Sm.) Welsh Wasatch Mts., Watson 225, 1869 (NY!).

***Lupinus tooelensis* C.P. Sm.** Sp. Lupinorum 640. 1948. Fabaceae. = *L. prunophilus* Jones Tooele Co., Deep Creek Mts., Cottam 7203, 1937 (UT!).

***Lupinus watsonii* Heller** Muhlenbergia 1: 114. 1905. Fabaceae. = *L. caespitosus* Nutt. Summit Co., Parleys Park, Watson 234, 1869 (US!).

Lychnis kingii Wats. Proc. Amer. Acad. 12: 247. 1877. Caryophyllaceae. Summit Co., head Bear River, Watson 153,1869 (US!;NY!).

Lygodesmia entrada **Welsh & Goodrich** Great Basin Naturalist 40: 83. 1980. Asteraceae. Grand Co., Tusher Canyon, Welsh & Welsh 16725, 1978 (BRY!;UT!;NY!).

Lygodesmia grandiflora **(Nutt.) T. & G. var.** ***stricta*** Maguire Amer. Midl. Naturalist 37: 145. 1947. Asteraceae. Carbon Co., 1 mi s Price, Maguire 18417, 1940 (NY!;US!;UTC!).

Lygodesmia juncea **(Pursh) D. Don var.** ***dianthopsis*** **D.C. Eaton** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 200. 1871. Asteraceae. = *L. dianthopsis* (D.C. Eaton) Tomb Davis (?) Co., Great Salt Lake Islands, Watson 707, 1869 (US!).

Machaeranthera commixta **Greene** Pittonia 4: 71. 1899. Asteraceae. Syn: *M. leptophylla* Rydb.? Garfield Co., Bromide Pass, Jones 5695v, 1894 (US!).

Machaeranthera glabriuscula **(Nutt.) Cronq. & Keck var.** ***confertiflora*** **Cronq.** Leafl. W. Bot. 10: 11. 1963. Asteraceae. = *Xylorhiza confertiflora* (Cronq.) T.J. Watson Garfield Co., 11 mi ne Henrieville, Cronquist 9164, 1961 (NY!;UTC!).

Machaeranthera kingii **(D.C. Eaton) Cronq. & Keck var.** ***barnebyana*** **Welsh & Goodrich** in Welsh Brittonia 33: 299. 1981. Asteraceae. Millard Co., Canyon Mts., Goodrich 14929, 1980 (BRY!;GH!;NY!;US!;RM!;UC!;USFS!;UT!;UTC!).

Machaeranthera latifolia **A. Nels.** Proc. Biol. Soc. Washington 20: 38. 1907. Asteraceae. Syn: *M. rubricaulis* Rydb.; *Aster rubrotinctus* Blake = *M. bigelovii* Gray ? Salt Lake Co., Big Cottonwood Canyon, Garrett 1933, 1906 (US!;RM!;UT!).

Machaeranthera leptophylla **Rydb.** Bull. Torrey Bot. Club 37: 147. 1910 Asteraceae. = *M. commixta* Greene? Cache Co., Logan, Rydberg sn, 1895 (NY!;BRY!).

Machaeranthera paniculata **A. Nels.** Proc. Biol. Soc. Washington 20: 38. 1907. Asteraceae. = *M. bigelovii* Gray ? Salt Lake Co., Parleys Canyon, Garrett 2083, 1906 (US!;RM!;UT!).

Machaeranthera pulverulenta **var.** ***vacans*** **A. Nels.** Bot. Gaz. 56: 70. 1913. Asteraceae. = *M. canescens* (Pursh) Gray? San Juan Co., Walker 360, 1912 (RM!;NY!).

Machaeranthera tortifolia **(T. & G.) Cronq. & Keck var.** ***imberbis*** **Cronq.** Leafl. W. Bot. 10: 12. 1963. Asteraceae. = *Xylorhiza tortifolia* var. *imberbis* (Cronq.) T.J. Watson Grand Co., w Moab, Cronquist 8994, 1961 (NY!;UTC!).

Macronema obovatum **Rydb.** Bull. Torrey Bot. Club 27: 618. 1900. Asteraceae. = *Haplopappus rydbergii* Blake Salt Lake Co., City Creek Canyon, Jones 1081, 1895 (US!;CAS!;RM!;POM!;NY!;UTC!).

Madronella oblongifolia **Rydb.** Bull. Torrey Bot. Club 36: 686. 1909. Lamiaceae. = *Monardella odoratissima* Benth. Juab Co., Mt. Nebo, Rydberg & Carlton 7706, 1905 (NY!;US!;RM!).

Madronella sessilifolia **Rydb.** Bull. Torrey Bot. Club 36: 685. 1909. Lamiaceae. = *Monardella odoratissima* Benth. Washington Co., St. George, Palmer 393, 1877 (NY!).

Mammillaria chlorantha **Engelm.** in Wheeler Rep. U.S. Geogr. Surv. W. 100th Meridian 6: 127. 1878. Cactaceae. = *Coryphantha vivipara* var. *deserti* (Engelm.) W.T. Marshall Washington Co., e St. George, Parry sn, 1874 (ISC!;BRY!).

Mentzelia albicaulis **Dougl. in Hook. var.** ***integrifolia*** Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 114. 1871. Loasaceae. = *M. dispersa* Wats. Davis Co., Antelope Island, Watson 430, 1869 (US!;NY!).

Mentzelia argillosa **Darlington** Ann. Missouri Bot. Gard. 21: 153. 1934. Loasaceae. Sevier Co., Vermillion, Jones 5631, 1894 (MO;POM!;US!).

Mentzelia multiflora **(Nutt.) Gray var.** ***integra*** **Jones** Proc. Calif. Acad. Sci II, 5: 689. 1895. Loasaceae. = *M. integra* (Jones) Tidestr. Washington Co., Rockville, Jones 6082C, 1894 (US!).

Mentzelia pterosperma **Eastw.** Proc. Calif. Acad. II, 6: 290. 1896. Loasaceae. San Juan Co., Willow Creek, Eastwood 31, 1895 (CAS!).

Mertensia brevistyla Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 239. 1871. Boraginaceae. Summit (?) Co., Wasatch Mts., Watson 845, 1869 (NY!).

Mertensia leonardii **Rydb.** Bull. Torrey Bot. Club 36: 681. 1909. Boraginaceae. = *M. arizonica* Greene var. *leonardii* (Rydb.) Johnst. Salt Lake Co., Mill Creek Canyon, Leonard sn, 1884 (NY!).

Mertensia paniculata var. ***nivalis*** Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 239. 1871. Boraginaceae. = *M. viridis* A. Nels. var. *cana* (Rydb.) L.O. Williams Summit Co., Bear River Canon, Watson 844, 1869 (CAS!;US!;NY!).

Mertensia praecox **Smiley in Macbr.** Contr. Gray Herb. II, 48: 10. 1916. Boraginaceae. = *M. oblongifolia* var. *nevadensis* (A. Nels.) L.O. Williams Cache Co., Logan Canyon, Smith 2160, 1910 (UTC!).

Mertensia sampsonii **Tidestr.** Proc. Biol Soc. Washington 26: 122. 1913. Boraginaceae. = *M. arizonica* var. *leonardii* (Rydb.) Johnst. Sanpete Co., e of Ephraim, Sampson 677, (US!).

Mertensia toyabensis **var.** ***subnuda*** **Macbr.** Contr. Gray Herb. II, 48: 7. 1916. Boraginaceae. = *M. arizona* var. *subnuda* (Macbr.) L.O. Williams Wayne Co. (?), Fish Lake Mountain, Ward 329, 1875 (GH).

Micropuntia barkleyana **Daston** Amer. Midl. Naturalist 36: 662. 1946. Cactaceae. = *Opuntia pulchella* Engelm. Millard Co., Desert Experimental Range, Marsh sn, 1945 (F?).

Micropuntia brachyrohopalica **Daston** Amer. Midl. Naturalist 36: 661. 1946. Cactaceae. = *Opuntia pulchella* Engelm. Millard Co., Desert Experimental Range, Marsh sn, 1945 (F?).

Micropuntia spectatissima **Daston** Amer. Midl. Naturalist 36: 661. 1946. Cactaceae. = *Opuntia pulchella Engelm.* Millard Co., Desert Experimental Range, Marsh sn, 1946 (F?).

Mimulus eastwoodiae **Rydb.** Bull. Torrey Bot. Club 40: 483. 1913. Scrophulariaceae. San Juan Co., San Juan River, near Bluff, Rydberg 9883, 1911 (NY!;US!;RM!;UT!).

Mimulus glabratus **H.B.K. ssp.** ***utahensis*** **Pennell** Acad. Nat. Sci. Philadelphia Monogr. 1: 123. 1935. Scrophulariaceae. = *M. glabratus* H.B.K. Millard Co., Preuss Lake, Tidestrom 11180, 1919 (PH).

Mimulus parryi Gray Proc. Amer. Acad. 11: 97. 1876. Scrophulariaceae. Washington Co., near St. George, Parry 147, 1874 (NY!;US!;ISC!;NDG!).

***Mirabilis glutinosa* A. Nels.** Proc. Biol. Soc. Washington 17: 92. 1904. Nyctaginaceae. = *M. bigelovii* Gray var. *retrorsa* (Heller) Munz Washington Co., near St. George, Goodding 778, 1902 (RM!).

***Mitella stenopetala* Piper** Erythea 7: 161. 1899. Saxifragaceae. = *M. stauropetala* Piper Salt Lake (?) Co., Wasatch Mts., Watson 365, 1869 (?).

***Muhlenbergia curtifolia* Scribn.** Bull. Torrey Bot. Club 38: 328. 1911. Poaceae. = *M. thurberi* Rydb. Kane Co., inter Kanab & Carmel, Jones 6077j, 1894 (US!).

***Najas flexilis* ssp. *caespitosus* Maguire in Maguire & Jensen** Rhodora 44: 7. 1942. Najadaceae. = *N. caespitosus* (Maguire) Reveal Sevier Co., Pelican Point, Fish Lake, Maguire 19888, 1940 (UTC!;BRY!).

***Nasturtium obtusum* Nutt. var. *alpinum* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 15. 1871. Brassicaceae. = *Rorippa curvipes* var. *alpina* (Wats.) Stuckey Summit Co., head of Bear River Canyon, Uinta Mts., Watson 60, 1869 (US!).

***Navarretia setosissima* T. & G. in Ives** Rep. Colorado Riv. W. 4: 22. 1860. Polemoniaceae. = *Langloisia setosissima* (T. & G.) Greene Washington Co., Virgin River, Fremont 414, (NY!).

Nemophila breviflora Gray Proc. Amer. Acad. 10: 315. 1875. Hydrophyllaceae. Summit Co., Parleys Park, Watson 169, 1869 (NY!;US!).

***Notholaena parryi* D.C. Eaton** Amer. Naturalist 9: 351. 1875. Polypodiaceae. Washington Co., St. George, Parry 263, 1874 (US!;ISC!;BRY!).

***Nuttallia lobata* Rydb.** Bull. Torrey Bot. Club 40: 61. 1913. Loasaceae. = *Mentzelia integra* (Jones) Tidestr. Washington Co., near St. George, Palmer 172, 1877 (NY!).

***Oenothera acutissima* W.L. Wagner** Systematic Botany 6: 153. 1981. Onagraceae. Daggett Co., Greendale Campground, Neese & Peterson 5428, 1978 (BRY!).

***Oenothera albicaulis* Pursh var. *decumbens* Wats. ex Parry** Amer. Naturalist 9: 270. 1875. Onagraceae. = *O. deltoides* ssp. *ambigua* (Wats.) W. Klein Washington Co., near St. George, Parry 63, 1874 (GH?).

***Oenothera alyssoides* H. & A. var. *minutiflora* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 111. 1871. Onagraceae. = *Camissonia minor* (A. Nels.) Raven Tooele Co., Stansbury Island, Watson 421, 1869 (US!).

***Oenothera alyssoides* Pursh var. *villosa* Wats.** Proc. Amer. Acad. 8: 591. 1873. Onagraceae. = *Camissonia boothii* ssp. *alyssoides* (H. & A.) Raven Salt Lake (?) Co., near Salt Lake, Stansbury sn, 1850 (NY!).

***Oenothera ambigua* Wats.** Proc. Amer. Acad. 14: 293. 1879. Onagraceae. = *O. deltoides* var. *ambigua* (Wats.) Munz Washington Co., near St. George, Palmer 162, 1877 (US!;ISC!).

***Oenothera brevipes* var. *parviflora* Wats. in Parry** Amer. Naturalist 9: 271. 1875. Onagraceae. = *Camissonia multijuga* (Wats.) Raven Washington Co., near St. George, Parry 74, 1874 (GH;MO;F).

***Oenothera caespitosa* Nutt. var. *jonesii* Munz** Amer. J. Bot. 18: 731. 1931. Onagraceae. Syn: *O. caespitosa* ssp. *jonesii* (Munz) Munz Tooele Co., Fish Springs, Jones sn, 1891 (POM!).

***Oenothera californica* ssp. *avita* W. Klein** Aliso 5: 179. 1962. Onagraceae. = *O. avita* (W. Klein) W. Klein Washington Co., 0.5 ne of Leeds, Klein 1049, 1959 (RSA).

***Oenothera gauraeflora* var. *hitchcockii* H. Lev.** Monogr. Oenothera 226. 1905. Onagraceae. = *Camissonia boothii* ssp. *alyssoides* (H. & A.) Raven Simpsons Park, without coll., 1859 (MO).

***Oenothera hookeri* T. & G. var. *angustifolia* Gates** Mut. Factors Evol. 10: 30. 1915. Onagraceae. Utah Co., Asphalt (s Thistle), Jones 5624, 1894 (US!;NY!).

***Oenothera johnsonii* Parry** Amer. Nat. 9: 270. 1875. Onagraceae. = *O. primiveris* Gray Washington Co., near St. George, Parry 64, 1874 (ISC!).

***Oenothera longissima* Rydb.** Bull. Torrey Bot. Club 40: 65. 1913. Onagraceae. San Juan Co., Natural Bridges Rydberg & Garrett 9410, 1911 (NY!;US!).

***Oenothera multijuga* Wats.** Amer. Naturalist 7: 300. 1873. Onagraceae. = *Camissonia multijuga* (Wats.) Raven Kane Co., near Kanab, Thompson sn, 1872 (NY?).

***Oenothera multijuga* Wats. var. *orientalis* Munz** Amer. J. Bot. 15: 232. 1928. Onagraceae. = *Camissonia walkeri* ssp. *walkeri* Grand Co., Moab, Jones sn, 1913 (POM!).

***Oenothera parryi* Wats. ex Parry** Amer. Naturalist 9: 270. 1875. Onagraceae. = *Camissonia parryi* (Wats.) Raven Washington Co., near St. George, Parry 72, 1874 (US!;NY!;BRY!;ISC!;NDG!).

***Oenothera scapoidea* Nutt. in T. & G. ssp. *utahensis* Raven** Univ. Calif. Publ. Bot. 34: 96. 1962. Onagraceae. = *Camissonia scapoidea* ssp. *utahensis* (Raven) Raven Salt Lake Co., Black Rock, Watson 414, 1869 (US!).

***Oenothera tenuissima* Jones** Proc. Calif. Acad. II, 5: 683. 1895. Onagraceae. = *Camissonia parryi* (Wats.) Raven Washington Co., Rockville, Jones 6083, 1894 (POM!;US!;RM!;NY!).

***Oenothera triloba* var. *ecristata* Jones** Proc. Calif. Acad. II, 5: 681. 1895. Onagraceae. = *O. flava* (A. Nels.) Garrett Garfield Co., Panguitch Lake, Jones 60155, 1894 (POM!).

***Opuntia barbata* M. Brandegee ex J.A. Purpus** Monats. Kakteenk. 10: 97. 1900. Cactaceae. = *O. polyacantha* (?) Haw. San Juan (?) Co., La Sal Mts., Purpus sn, 1897 (?).

***Opuntia barbata* M. Brandegee ex J.A. Purpus var. *gracillima* M. Brandegee ex J.A. Purpus** Monats. Kakteenk. 10: 110, 120. 1900. Cactaceae. = *O. polyacantha* (?) Haw. San Juan (?) Co., La Sal Mts., Purpus sn, 1897 (?).

***Opuntia basilaris* Engelm. & Bigel. var. *woodburyi* Earl** Sahuaroland Bull. 34: 15. 1980. Cactaceae. Washington Co., Fort Pierce Wash, Woodbury 2060a, 1977 (BRY!).

***Opuntia palmeri* Engelm.** Contr. U.S. Natl. Herb. 3: 423. 1896. Cactaceae. = ? *O. phaeacantha* var. *discata* (Griffiths) Benson & Walkington Washington Co., near St. George, Palmer sn, 1877 (MO).

***Opuntia rubrifolia* Engelm.** Contr. U.S. Natl. Herb. 3: 424. 1896. Cactaceae. = *O. erinacea* var. *ursina* Parish Washington Co., near St. George, Palmer 3, 1877 (MO).

***Opuntia utahensis* J.A. Purpus** Monats. Kakteenk. 19: 133. 1909. Cactaceae. = *O. macrorhiza* Engelm. San Juan (?) Co., La Sal Mts., Purpus sn, 1897 (US!).

***Oreocarya breviflora* Osterh.** in Payson Univ. Wyoming Publ. Bot. 1: 169. 1926. Boraginaceae. = *Cryptantha breviflora* (Osterh.) Payson Uintah Co., n Jensen, Osterhout 6414, 1925 (RM!;BRY!).

***Oreocarya commixta* Macbr.** Contr. Gray Herb. II, 48: 33. 1916. Boraginaceae. = *Cryptantha humilis* var. *commixta* (Macbr.) Higgins Juab Co., Juab, Goodding 1074, 1902 (GH;RM!).

***Oreocarya disticha* Eastw.** Bull. Torrey Bot. Club 30: 258. 1903. Boraginaceae. Syn: *Cryptantha jamesii* var. *disticha* (Eastw.) Payson = *C. cinerea* (Greene) Cronq. San Juan Co., Bartons range, Eastwood sn, 1895 (CAS!;NY!).

***Oreocarya dolosa* Macbr.** Contr. Gray Herb. II, 48: 32. 1916. Boraginaceae. = *Cryptantha humilis* var. *shantzii* (Tidestr.) Higgins Cache Co., Logan, Smith 1605, 1909 (RM!).

***Oreocarya jonesiana* Payson** Univ. Wyoming Publ. Bot. 1: 168. 1926. Boraginaceae. = *Cryptantha jonesiana* (Payson) Payson Emery Co., San Rafael Swell, Jones sn, 1914 (RM!;POM!;BRY!).

***Oreocarya pustulosa* Rydb.** Bull. Torrey Bot. Club 40: 480. 1913. Boraginaceae. = *Cryptantha pustulosa* (Rydb.) Payson Syn: *C. jamesii* var. *pustulosa* (Rydb.) Harrington San Juan Co., Elk Mts., Rydberg & Garrett 9320, 1911 (NY!).

***Oreocarya rugulosa* Payson** Univ. Wyoming Publ. Bot. 1: 166. 1926. Boraginaceae. = *Cryptantha rugulosa* (Payson) Payson Tooele Co., Fish Springs, Jones sn, 1891 (GH;RM!;POM!).

***Oreocarya shantzii* Tidestr.** Proc. Biol. Soc. Washington 26: 122. 1913. Boraginaceae. = *Cryptantha humilis* var. *shantzii* (Tidestr.) Higgins Salt Lake Co., s Great Salt Lake, Kearney & Shantz 3098, 1912 (US!).

***Oreocarya tenuis* Eastw.** Bull. Torrey Bot. Club 30: 244. 1903. Boraginaceae. = *Cryptantha tenuis* (Eastw.) Payson Grand Co., Courthouse Wash, Eastwood sn, 1892 (CAS!;RM!;NY!).

***Oreocarya torva* A. Nels.** Amer. J. Bot. 23: 269. 1936. Boraginaceae. = *Cryptantha flava* (A. Nels.) Payson Carbon Co., Price, Flowers 6395, 1933 (UT!).

***Oreocarya wetherillii* Eastw.** Bull. Torrey Bot. Club 30: 242. 1903. Boraginaceae. = *Cryptantha wetherillii* (Eastw.) Payson Grand Co., Courthouse Wash, Eastwood sn, 1892 (CAS!;RM;NY!).

***Oreocarya williamsii* A. Nels.** Amer. J. Bot. 21: 578. 1934. Boraginaceae. = *Cryptantha stricta* (Osterh.) Payson Daggett Co., Flaming Gorge, Williams 489, 1932 (RM!;NY!).

***Orogenia linearifolia* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 120. 1871. Apiaceae. Summit Co., Wasatch Mts., north of Parleys Park, Watson 440, 1869 (US!;NY!).

***Oxybaphus angustifolia* var. *viscidus* Eastw.** Proc. Calif. Acad. II, 6: 313. 1896. Nyctaginaceae. = *O. linearis* (Pursh) Robins. San Juan Co., Butler Spring, Eastwood 101, 1895 (CAS!).

***Oxybaphus glaber* Wats.** Amer. Naturalist 7: 301. 1873. Nyctaginaceae. Kane Co., Kanab, Thompson sn, 1872 (US!).

***Oxytropis jonesii* Barneby** Proc. Calif. Acad. IV, 27: 215. 1952. Fabaceae. Garfield Co., Red Canyon, Ripley & Barneby 8550, 1947 (CAS!).

***Oxytropis oreophila* Gray var. *juniperina* Welsh** Great Basin Naturalist 38: 339. 1978. Fabaceae. Wayne Co., 1 mi e Bicknell, Welsh & Moore 13828, 1976 (BRY!;UT!;ISC!).

***Pachylophus crinitis* Rydb.** Fl. Rocky Mts. 598, 1064. 1917. Onagraceae. = *Oenothera caespitosa* var. *crinita* (Rydb.) Munz Wayne Co., Rabbit Valley, Ward 526, 1875 (US!).

***Paronychia pulvinata* Gray var. *longiaristata* Chaudri** Revis. Paronychia 194. 1968. Caryophyllaceae. Duchesne Co., Mt. Emmons, Hermann 5041, 1933 (BRY!).

***Parrya platycarpa* Rydb.** Bull. Torrey Bot. Club 39: 326. 1912. Brassicaceae. = *P. rydbergii* Botsch. Summit (?) Co., Uinta Mts, Watson 54, 1869 (US!;NY!).

***Parthenium alpinum* (Nutt.) T. & G. var. *ligulatum* Jones** Contr. W. Bot. 13: 16. 1910. Asteraceae. Syn: *Bolophyta ligulata* (Jones) W.A. Weber = *P. ligulatum* (Jones) Barneby Duchesne Co., Theodore, Jones sn, 1908 (POM!;US!;CAS!;BRY!).

***Pediocactus despainii* Welsh & Goodrich** Great Basin Naturalist 40: 83. 1980. Cactaceae. Emery Co., San Rafael Swell, Despain 266a, 1978 (BRY!;NY!).

***Pediocactus hermannii* W.T. Marshall** Saguaroland Bull. 8: 78. 1954. Cactaceae. = *P. simpsonii* (Engelm.) Britt. & Rose Garfield Co., Hatch, Hermann & Hermann sn, 1953 (BRY!).

***Pediocactus winkleri* Heil** Cact. & Succ. J. (U.S.) 51: 28. 1979. Cactaceae. Wayne Co., Winkler sn, (UNM).

***Penstemon abietinus* Pennell** Contr. U.S. Natl. Herb. 20: 376. 1920. Scrophulariaceae. Sevier Co., Irelands Ranch, Jones 5440, 1894 (US!;RM!;BRY!;NY!).

***Penstemon acuminatus* Dougl. var. *congestus* Jones** Proc. Calif. Acad. II, 5: 714. 1895. Scrophulariaceae. Syn: *P. pachyphyllus* ssp. *congestus* (Jones) Keck; do var. *congestus* (Jones) N. Holmgr. = *P. congestus* (Jones) Pennell Washington Co., near Cannan Ranch, Rockwell, Jones 5262, 1894 (POM!;US!).

***Penstemon angustifolius* Nutt. var. *vernalensis* N. Holmgren** Brittonia 31: 229. 1978. Scrophulariaceae. Uintah Co., n Maeser, Holmgren et al. 8748, 1979 (NY!;BRY!;UTC!).

***Penstemon atwoodii* Welsh** Great Basin Naturalist 35: 378. 1976. Scrophulariaceae. Kane Co., sse Canaan Peak, Welsh & Welsh 12821, 1975 (BRY!;UT!;NY!;UTC!).

***Penstemon azureus* var. *ambiguus* Gray** Syn. Fl. N. Amer. 2: 272. 1886. Scrophulariaceae. = *P. sepalulus* A. Nels. Utah Co., near Provo, Watson 786, 1869 (US!;NY!).

***Penstemon bracteatus* Keck** Leafl. W. Bot. 1: 82. 1934. Scrophulariaceae. Garfield Co., Red Canyon, Eastwood & Howell 783, 1933 (CAS!).

***Penstemon caespitosus* Nutt. ex Gray ssp. *perbrevis* Pennell** Contr. U.S. Natl. Herb. 20: 375. 1920. Scrophulariaceae. Carbon Co., near Castle Gate, Pennell 6138, 1915 (NY!;US!).

***Penstemon caespitosus* Nutt. ex Gray var. *suffruticosus* Gray** Syn. Fl. N. Amer. 2: 270. 1878. Scrophulariaceae. = *P. tusharensis* N. Holmgren Beaver Co., near Beaver, Palmer sn, 1877 (ISC!).

***Penstemon carnosus* Pennell in Graham** Ann. Carnegie Mus. 25: 329. 1937. Scrophulariaceae. Emery Co., San Rafael Swell, Cottam 5229, 1935 (UT!;NY!;UTC!).

***Penstemon comarrhenus* Gray** Proc. Amer. Acad. 12: 81. 1876. Scrophulariaceae. Garfield (?) Co., Aquarius Plateau, Ward 462, 1875 (NY!;US!).

Penstemon concinnus Keck Amer. Midl. Naturalist 23: 608. 1940. Scrophulariaceae. Millard Co., Tunnel Springs Range, Cottam 5634, 1933 (CAS!;US!;UT!;NY!).

Penstemon confertus var. ***aberrans*** Jones Proc. Calif. Acad. II, 5: 715. 1895. Scrophulariaceae. = *P. procerus* var. *aberrans* (Jones) A. Nels. Wasatch Co., Soldier Summit, Jones 5601i, 1894 (POM!;US!).

Penstemon confusus Jones Zoe 4: 280. 1893. Scrophulariaceae. Juab Co., Detroit, Jones sn, 1891 (POM!;CAS!;BRY!).

Penstemon crandallii A. Nels. ssp. ***atratus*** Keck Bull. Torrey Bot. Club 64: 370. 1937. Scrophulariaceae. = *P. crandallii* var. *atratus* (Keck) N. Holmgren San Juan (?) Co., La Sal Mts., Jones sn, 1914 (CAS!;US!;POM!;NY!;BRY!).

Penstemon cyananthus Hook. ssp. ***compactus*** Keck Amer. Midl. Naturalist 23: 615. 1940. Scrophulariaceae. = *P. compactus* (Keck) Crosswhite Cache Co., Mt. Naomi, Maguire 16148, 1938 (UTC!).

Penstemon cyananthus Hook. ssp. ***longiflorus*** Pennell Contr. U.S. Natl. Herb. 20: 353. 1920. Scrophulariaceae. = *P. longiflorus* (Pennell) S. Clark Beaver Co., near Beaver, Palmer 376, 1877 (US!;NY!).

Penstemon dolius Jones ex Pennell Contr. U.S. Natl. Herb. 20: 341. 1920. Scrophulariaceae. Tooele Co., Deep Creek Mts., Jones sn, 1891 (POM!;BRY!).

Penstemon dolius Jones var. ***duchesnensis*** N. Holmgren Brittonia 31: 219. 1979. Scrophulariaceae. Duchesne Co., e Duchesne, Holmgren et al, 8762, 1978 (NY!;BRY!;UTC!).

Penstemon eatonii Gray Proc. Amer. Acad. 8: 395. 1872. Scrophulariaceae. Utah Co., Provo Canyon, Watson 776, 1869 (US!;NY!).

Penstemon eatonii Gray var. ***undosus*** Jones Proc. Calif. Acad. II, 5: 715. 1895. Scrophulariaceae. Syn: *P. eatonii* ssp. *undosus* (Jones) Keck Washington Co., St. George, Jones 51101h, 1894 (POM!;US!;NY!).

Penstemon garrettii Pennell Contr. U.S. Natl. Herb. 20: 353. 1920. Scrophulariaceae. = *P. scariosus* Pennell sens. lat. Wasatch Co., near Midway, Carlton & Garrett 6697, 1905 (NY!;US!).

Penstemon glaber var. ***utahensis*** Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 217. 1871. Scrophulariaceae. = *P. subglaber* Rydb. Summit Co., Uinta Mts, Watson 771, 1869 (US!;NY!).

Penstemon goodrichii N. Holmgren Brittonia 30: 416. 1978. Scrophulariaceae. Uintah Co., e Lapoint, Holmgren et al 8760, 1978 (NY!;BRY!;UTC!).

Penstemon grahamii Keck in Graham Ann. Carnegie Mus. 26: 331. 1937. Scrophulariaceae. Uintah Co., Sand Wash, Graham 7883, 1933 (CM!).

Penstemon heterophyllus var. ***latifolius*** Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 222. 1871. Scrophulariaceae. = *P. platyphyllus* Rydb. Salt Lake Co., Cottonwood Canyon, Watson 787, 1869 (US!).

Penstemon humilis Nutt. in Gray var. ***brevifolius*** Gray Syn. Fl. N. Amer. 2(1): 267. 1878. Scrophulariaceae. Salt Lake Co., Cottonwood Canyon, Watson 781, 1869 (US!;NY!).

Penstemon jonesii Pennell (hybrid) Contr. U.S. Natl. Herb. 20: 338. 1920. Scrophulariaceae. = *P. eatonii x P. leiophyllus* Washington Co., Springdale, Jones 5250, 1894 (US!).

Penstemon laevis Pennell Contr. U.S. Natl. Herb. 20: 347. 1920. Scrophulariaceae. Washington Co., Springdale, Jones 5250, 1894 (US!;POM!).

Penstemon leiophyllus Pennell Contr. U.S. Natl. Herb. 20: 346. 1920. Scrophulariaceae. Garfield Co., Mammoth Creek, Jones 6026b, 1894 (US!).

Penstemon lentus Pennell ssp. ***albiflorus*** Keck Amer. Midl. Naturalist 23: 616. 1940. Scrophulariaceae. San Juan Co., 8 mi w Blanding, Porter 1801, 1939 (RM!;NY!;UTC!).

Penstemon leonardii Rydb. Bull. Torrey Bot. Club 40: 483. 1913. Scrophulariaceae. Wasatch Mts., Leonard sn, 1884 (NY!).

Penstemon leptanthus Pennell Contr. U.S. Natl. Herb. 20: 339. 1920. Scrophulariaceae. Sanpete Co., Twelve Mile Creek, Ward 280, 1875 (US!).

Penstemon linarioides Gray in Torr. var. ***sileri*** Gray Syn. Fl. N. Amer. 2(1): 270. 1878. Scrophulariaceae. Kane (?) Co., S. Utah, Siler sn, 1873 (NY!).

Penstemon mucronatus N. Holmgren Brittonia 31: 234. 1979. Scrophulariaceae. Daggett Co., s. Manila, Holmgren et al. 8447, 1978 (NY!;BRY!;UTC!).

Penstemon nanus Keck Amer. Midl. Naturalist 23: 607. 1940. Scrophulariaceae. Millard Co., Desert Experimental Range, Plummer 7313, 1939 (CAS!;BRY!;UT!;NY!;UTC!).

Penstemon navajoa N. Holmgren Brittonia 30: 419. 1978. Scrophulariaceae. San Juan Co., Navajo Mt., N. & P Holmgren 8587, 1977 (NY!;BRY!;UTC!).

Penstemon obtusifolius Pennell Contr. U.S. Natl. Herb. 20: 370. 1920. Scrophulariaceae. = *P. humilis* var. *obtusifolius* (Pennell) Reveal Washington Co., Springdale, Jones 5249am, 1894 (US!;POM!;NY!).

Penstemon ophianthus Pennell Contr. U.S. Natl. Herb. 20: 343. 1920. Scrophulariaceae. Syn: *P. jamesii* ssp. *ophianthus* (Pennell) Keck Wayne Co., Thurber, Jones 5708, 1894 (US!;POM!;NY!).

Penstemon palmeri Gray ssp. ***eglandulosus*** Keck Amer. Midl. Naturalist 18: 797. 1937. Scrophulariaceae. = *P. palmeri* var. *eglandulosus* (Keck) N. Holmgren Kane Co., 2.5 mi n Kanab, Maguire et al. 12279, 1935 (RM!;NY!;UTC!).

Penstemon parvus Pennell Contr. U.S. Natl. Herb. 20: 345. 1920. Scrophulariaceae. Garfield Co., Aquarius Plateau, Ward 546, 1875 (US!).

Penstemon patricus N. Holmgren Brittonia 31: 238. 1979. Scrophulariaceae. Juab Co., Thoms Creek Canyon, Holmgren et al. 9018, 1978 (NY!;BRY!;UT!;UTC!).

Penstemon phlogifolius Greene Leafl. Bot. Obs. & Crit. 1: 164. 1906. Scrophulariaceae. = *P. watsonii* Gray Carbon Co., Castle Gate, Jones 5486s, 1894 (US!;POM!).

Penstemon platyphyllus Rydb. Bull. Torrey Bot. Club 36: 690. 1909. Scrophulariaceae. Syn: *P. heterophyllus* var. *latifolius* Wats. Salt Lake Co., Cottonwood Canyon, Watson 787, 1869 (US!).

Penstemon pseudohumilis Jones Contr. W. Bot. 12: 65. 1908. Scrophulariaceae. = *P. marcusii* (Keck) N. Holmgren? Carbon Co., Price, Jones sn, 1898 (POM!).

Penstemon pumilus var. ***thompsoniae*** Gray Syn. Fl. N. Amer. 2(1): 269. 1878. Scrophulariaceae. Syn: *P. caespitosus* var. *thompsoniae* (Gray) A. Nels. = *P. thompsoniae* (Gray) Rydb. Kane Co., Kanab, Thompson sn, 1872 (GH).

Penstemon scariosus Pennell Contr. U.S. Natl. Herb. 20: 353. 1920. Scrophulariaceae. Syn: *P. garrettii* Pennell Sanpete Co., Musinia Peak, Tidestrom 568, 1907 (US!).

Penstemon tidestromii Pennell Contr. U.S. Natl. Herb. 20: 379. 1920. Scrophulariaceae. Sanpete Co., San Pitch Mts., Tidestrom 1296, 1908 (US!).

Penstemon uintahensis Pennell Contr. U.S. Natl. Herb. 20: 350. 1920. Scrophulariaceae. Uintah Co., Dyer Mine, Goodding 1221, 1902 (US!;RM!;BRY!;NY!).

Penstemon utahensis Eastw. Zoe 4: 124. 1893. Scrophulariaceae. San Juan Co., n Monticello, Eastwood sn, 1892 (CAS!;US!).

Penstemon wardii Gray Proc. Amer. Acad. 12: 82. 1876. Scrophulariaceae. Sevier Co., near Glenwood, Ward 162, 1875 (US!;NY!).

Petalonyx parryi Gray Proc. Amer. Acad. 10: 77. 1874. Loasaceae. Washington Co., St. George ("within a stones throw of the great Mormon temple"), Parry 75, 1874 (NY!;BRY!;ISC!).

Petalostemon flavescens Wats. Amer. Naturalist 7: 299. 1873. Fabaceae. = *Dalea flavescens* (Wats.) Welsh Kane Co., "Kanab," Thompson sn, 1871 (US!).

Peteria thompsonae Wats. Amer. Naturalist 7: 300. 1873. Fabaceae. Kane Co., Kanab, Thompson sn, 1872 (GH;US!;NY!;BRY!).

Peucedanum bicolor Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 129. 1871. Apiaceae. = *Lomatium bicolor* (Wats.) Coult. & Rose Summit Co., Parleys Park, Watson 467, 1869 (US!;NY!).

Peucedanum graveolens Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 128. 1871. Apiaceae. = *Lomatium nuttallii* (Gray) Macbr. Wasatch Mts., Watson 463, 1869 (US!;NY!).

Peucedanum juniperinum Jones Contr. W. Bot. 8: 29. 1898. Apiaceae. = *Lomatium juniperinum* (Jones) Coult. & Rose Summit Co., Coalville, Jones sn, 1889 (POM!;US!;BRY!).

Peucedanum lapidosum Jones Zoe 2: 246. 1891. Apiaceae. = *Cymopterus longipes* Wats. Summit Co., Echo, Jones sn, 1890 (US!;RM!;POM!).

Peucedanum millefolium Wats. Rep. U.S. Explor. 40th Parallel, Bot. 5: 129. 1871. Apiaceae. = *Lomatium grayi* Coult. & Rose Davis Co., Antelope Island, Watson 466, 1869 (NY!;US!).

Peucedanum parryi Wats. Proc. Amer. Acad. 11: 143. 1876. Apiaceae. = *Lomatium parryi* (Wats.) Macbr. Washington (?) Co., Southern Utah, Parry 85, 1874 (NY!).

Peucedanum triternatum var. ***platycarpum*** Torr. in Standb. Explor. Great Salt Lake 389. 1852. Apiaceae. = *Lomatium triternatum* var. *platycarpum* (Torr.) Cronq. Great Salt Lake, Stansbury sn, 1850 (NY!).

Phaca mollissima var. ***utahensis*** Torr. in Stansb. Explor. Great Salt Lake 385. 1852. Fabaceae. = *Astragalus utahensis* (Torr.) T. & G. Tooele Co., w shore Stansbury Island, Great Salt Lake, Stansury sn, 1850 (NY!).

Phaca pardalina Rydb. N. Amer. Fl. 24: 352. 1929. Fabaceae. = *Astragalus pardalinus* (Rydb.) Barneby Emery Co., Cedar Mt., Jones sn, 1915 (NY!;POM!).

Phacelia argillacea Atwood Phytologia 26: 437. 1973. Hydrophyllaceae. Utah Co., Spanish Fork Canyon, Atwood et al. 3091, 1971 (BRY!;UT!;NY!;US!;UTC!).

Phacelia cephalotes Gray Proc. Amer. Acad. 10: 325. 1875. Hydrophyllaceae. Washington Co., near St. George, Parry 179, 1874 (NY!;US!;BRY!;ISC!).

Phacelia demissa Gray var. ***heterotricha*** J.T. Howell Amer. Midl. Naturalist 29(1): 8. 1943. Hydrophyllaceae. Piute Co., Marysvale, Jones 5388o, 1894 (POM!;US!).

Phacelia foetida Goodding Bot. Gaz. 37: 58. 1904. Hydrophyllaceae. = *P. palmeri* Torr. Washington Co., Diamond Valley, Goodding 833, 1902 (RM!).

Phacelia howelliana Atwood Rhodora 74: 456. 1972. Hydrophyllaceae. San Juan Co., Bluff, Atwood 2454, 1970 (BRY!;RM!;NY!;US!;UTC!).

Phacelia incana Brand Beit. z. Kenntnis der Hydrophyll. 8. 1911. Hydrophyllaceae. Tooele Co., Dugway, Jones sn, 1891 (POM!;RM!;NY!).

Phacelia indecora J.T. Howell Amer. Midl. Naturalist 29: 12. 1943. Hydrophyllaceae. San Juan Co., Bluff, Jones sn, 1919 (CAS!).

Phacelia mammillariensis Atwood Phytologia 26: 437. 1973. Hydrophyllaceae. Kane Co., e Glen Canyon City, Welsh & Atwood 9809, 1970 (BRY!).

Phacelia nudicaulis Eastw. Zoe 4: 123. 1893. Hydrophyllaceae. = *P. demissa* Gray var. *demissa* Grand Co., near Moab, Eastwood sn, 1892 (CAS!;POM!;US!).

Phacelia orbicularis Rydb. Bull. Torrey Bot. Club 40: 479. 1913. Hydrophyllaceae. = *P. corrugata* A. Nels. Wayne Co., Marvine Laccolite, Jones 5663, 1894 (US!;NY!).

Phacelia palmeri Torr. in Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 251. 1871. Hydrophyllaceae. Syn: *P. foetida* Goodding Washington Co., near St. George, Palmer 4, 1870 (NY!;US!).

Phacelia pinetorum Jones Zoe 4: 279. 1893. Hydrophyllaceae. = *Eucrypta micrantha* Torr. Tooele or Juab Co., Deep Creek Mts., Jones sn, 1891 (POM!;CAS!).

Phacelia pulchella Gray Proc. Amer. Acad. 10: 326. 1875. Hydrophyllaceae. Washington Co., near St. George, Parry 182, 1874 (GH;POM!;NY!;US!;BRY!).

Phacelia pulchella Gray var. ***sabulonum*** J.T.Howell Amer. Midl. Naturalist 29: 12. 1943. Hydrophyllaceae. = *P. pulchella* Gray Kane Co., Kaiparowits Plateau, Tompkins sn, 1939 (CAS!).

Phacelia rafaelensis Atwood Rhodora 74: 454. 1972. Hydrophyllaceae. Wayne Co., Capitol Reef National Monument, Atwood & Higgins 1834, 1969 (BRY!;CAS!;RM!;NY!;US!;UTC!).

Phacelia rotundifolia Torr. ex Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 253. 1871. Hydrophyllaceae. Southern Utah, Palmer sn, 1870 (NY!;US!).

Phacelia utahensis Voss Bull. Torrey Bot. Club 64: 135. 1937. Hydrophyllaceae. Sanpete Co., Gunnison, Jones sn, 1910 (POM!).

Phlox austromontana Cov. Contr. U.S. Natl. Herb. 4: 151. 1893. Polemoniaceae. Washington Co., Beaverdam Mts., Bailey 1944, 1891 (US!).

Phlox austromontana Cov. var. ***prostrata*** E. Nels. Rev. W. N. Amer. Phloxes 19. 1899. Polemoniaceae. Syn: *P. jonesii* Wherry Washington Co., Silver Reef, Jones 5163y–z, 1894 (NY!;US!;RM!;POM!;BRY!).

Phlox caesia Eastw. Leafl. W. Bot. 2: 54. 1937. Polemoniaceae. = *P. gladiformis* (Jones) E. Nels. Garfield Co., Red Canyon, Eastwood & Howell 752, 1933 (CAS!).

Phlox canescens T. & G. in Beckwith Rep. U.S. Explor. & Surv. R.R. Pacific 2: 122. 1857. Polemoniaceae. = *P. hoodii* var. *canescens* (T. & G.) Peck Tooele Co., s Great Salt Lake, Beckwith 4, 1854 (NY!).

Phlox cluteana **A. Nels.** Amer. Botanist 28: 24. 1922. Polemoniaceae. San Juan Co., Navajo Mt., Clute 18, 1919(?).

Phlox densa **Brand** Pflanzenr. 4. Fam. 250. 83. 1907. Polemoniaceae. = *P. austromontana* Cov. Beaver Co., Frisco, Jones 2021, 1880 (US!;POM!;NY!;UTC!).

Phlox grahamii **Wherry** Brittonia 5: 63. 1943. Polemoniaceae. = *P. longifolia* Nutt. Uintah Co., Sand Wash, Graham 7884, 1933 (CM!).

Phlox jonesii **Wherry** Notul. Nat. Acad. Nat. Sci. Philadelphia 146: 8. 1944. Polemoniaceae. = *P. austromontana* var. *prostrata* E. Nels. Washington Co., Zion Canyon, Jones sn, 1923 (US!;CAS!;POM!).

Phlox longifolia **Nutt. var. *gladiformis*** **Jones** Proc. Calif. Acad. II, 5: 711. 1895. Polemoniaceae. = *P. gladiformis* (Jones) E. Nels. Iron Co., Cedar Canyon, Jones 5208c, 1894 (POM!;US!).

Physaria acutifolia **Rydb. var. *purpurea*** **Welsh & Reveal** Great Basin Naturalist 37: 345. 1977. Brassicaceae. Grand Co., near Sego, Welsh 6902, 1968 (BRY!).

Physaria chambersii **Rollins var. *membranacea*** **Rollins** Rhodora 41: 404. 1939. Brassicaceae. = *P. lepidota* var. *membranacea* (Rollins) Rollins Garfield Co., Red Canyon, Rollins & Chambers 2448, 1938 (GH; RM!;US!;NY!).

Physaria grahamii **Morton in Graham** Ann. Carnegie Mus. 26: 220. 1937. Brassicaceae. Uintah Co., Chandler Canyon, Graham 9976, 1935 (US!;CM!).

Physaria lepidota **Rollins** Brittonia 33: 335. 1981. Brassicaceae. Kane Co., between Kanab and Zion, Rollins & Rollins 79198, 1979 (GH).

Physaria newberryi **Gray var. *racemosa*** **Rollins** Brittonia 33: 339. 1981. Brassicaceae. Washington Co., 13.5 mi s St. George, Holmgren et al. 9183, 1979 (GH).

Pinus contorta **Dougl. ex Loud. var. *latifolia*** **Engelm.** ex Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 331. 1871. Pinaceae. = *P. contorta* Dougl. Summit Co., Uinta Mts., Watson 1110, 1869 (?).

Plantago major **L. var. *pachyphylla*** **Pilger** Feddes Repert. 18: 277. 1922. Plantaginaceae. = *P. major* L. Salt Lake Co., Salt Lake City, Jones 1030, 1879 (POM!;UT!).

Plantago myosuroides **Rydb.** Mem. New York Bot. Gard. 1: 369. 1900. Plantaginaceae. = *P. elongata* Pursh Salt Lake Co., Salt Lake Valley, near mouth of Jordan River, Watson 749, 1869 (US!).

Platystemon remotus **Greene** Pittonia 5: 190. 1903. Papaveraceae. = *P. californicus* Benth. Washington Co., near St. George, Parry 8, 1874 (CAS!;ISC!).

Platystemon rigidulus **Greene** Pittonia 5: 167. 1903. Papaveraceae. = *P. californicus* Benth. Washington Co., near St. George, Parry 8a, 1874 (CAS!).

Platystemon terminii **Fedde** Pflanzenr. 4. Fam. 104: 128. 1909. Papaveraceae. = *P. californicus* Benth. Washington Co., Diamond Valley, Jones 5121, 1894 (POM!;US!).

Pleurophragma platypodum **Rydb.** Bull. Torrey Bot. Club 34: 434. 1907. Brassicaceae. = *Thelypodium integrifolium* var. *gracilipes* Robins. Grand Co., Moab, Jones sn, 1891 (NY!;CAS!;RM!;US!;BRY!).

Poa eatonii **Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 386. 1871. Poaceae. = *P. fendleriana* (Steud.) Vasey Salt Lake Co., Cottonwood Canyon, Eaton 1891, 1869 (NY!).

Poa festucoides **Jones** Proc. Calif. Acad. II, 5: 723. 1895. Poaceae. = *Festuca thurberi* Vasey Garfield Co., Mt. Ellen, Jones 5671, 1894 (POM!;US!).

Poa longiligula **Scribn. & Will.** USDA Div. Agrostol. Circ. 9: 3. 1899. Poaceae. = *P. fendleriana* (Steud.) Vasey sens. lat. Washington Co., Silver Reef, Jones 5149at, 1894 (RM!;NY!;US!).

Poa scabriuscula **Williams** USDA Div. Agrostol. Circ. 10: 4. 1899. Poaceae. = *P. fendleriana* (Steud.) Vasey Sevier Co., s Glenwood, Ward 136, 1895 (US!).

Polemonium albiflorum **Eastw.** Bot. Gaz. 37: 437. 1904. Polemoniaceae. = *P. foliosissimum* var. *alpinum* Brand. Carbon Co., Scofield, Harkness sn, 1902 (CAS!;RM!).

Polemonium foliosissimum **Gray ssp. *albiflorum*** **var. *alpinuum*** **Brand** Pflanzenr. 4. Fam. 250: 34. 1907. Polemoniaceae. Syn: *P. albiflorum* Eastw.; *P. foliosissimum* ssp. *albiflorum* (Eastw.) Brand Salt Lake Co., Alta, Jones 1114, 1879 (NY!;POM!;UT!).

Polygala acanthoclada **Gray** Proc. Amer. Acad. 11: 73. 1876. Polygalaceae. Syn: *P. acanthoclada* var. *intricata* Eastw. San Juan Co., San Juan R., Brandegee sn, 1873 (NY!).

Polygala acanthoclada **Gray var. *intricata*** **Eastw.** Proc. Calif. Acad. II, 6: 283. 1896. Polygalaceae. = *P. acanthoclada* Gray San Juan Co., Willow Creek, Eastwood 10, 1895 (CAS!).

Polygonum minimum **Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 315. 1871. Polygonaceae. Summit Co., Uinta Mts., Watson 1058, 1869 (US!).

Polygonum utahense **Brenckle & Cottam** Bull. Univ. Utah 30: 3. 1940. Polygonaceae. Garfield Co., 6 m n Escalante, Cottam 6507, 1935 (UT!;US!;BRY!;CAS!; RM!;UTC!).

Potamogeton pusillus **L. var. *vulgaris*** **subvar. *interruptus*** **J.W. Robbins** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 338. 1871. Potamogetonaceae. = *P. pusillus* var. *pusillus* Summit Co., Parleys Park, Silver Cr., Watson 1137, 1869 (NY!).

Potentilla dissecta **var. *decurrens*** **Wats.** Proc. Amer. Acad. 8: 557. 1873. Rosaceae. Syn: *P. decurrens* (Wats.) Rydb. = *P. ovina* var. *decurrens* (Wats.) Welsh & Johnston Summit Co.?, Uinta Mts., Watson 329, 1869 (US!).

Potentilla diversifolia **var. *pinnatisecta*** **Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 87. 1871. Rosaceae. = *P. ovina* Macoun Summit Co., Uinta Mts., Watson 331, 1869 (NY!).

Potentilla modesta **Rydb.** N. Amer. Fl. 22: 331. 1908. Rosaceae. = *P. concinna* var. *modesta* (Rydb.) Welsh & Johnston Piute Co., Mt. Barrette, near Marysvale, Rydberg & Carlton 7261, 1905 (NY!).

Potentilla paucijuga **Rydb.** N. Amer. Fl. 22: 348. 1908. Rosaceae. = *P. pensylvanica* var. *paucijuga* (Rydb.) Welsh & Johnston Grand (?) Co., La Sal Mts., Purpus 251, 1899 (NY!).

Potentilla pectinisecta **Rydb.** Bull. Torrey Bot. Club 24: 7. 1897. Rosaceae. = *P. gracilis* Dougl. Salt Lake Co., Salt Lake City, Jones 1765, 1880 (RM!;NY!;BRY!).

Potentilla proxima **Rydb.** N. Amer. Fl. 22(4): 339. 1908. Rosaceae. = *P. concinna* var. *proxima* (Rydb.) Welsh & Johnston Piute Co, s Belknap Peak, Rydberg & Carlton 7369, 1905 (NY!).

Potentilla sabulosa Jones Proc. Calif. Acad. Sci. II, 5: 680. 1895. Rosaceae. = *Ivesia sabulosa* (Jones) Keck Garfield Co., Sevier River, Jones 6032, 1894 (US!; POM!;CAS!;RM!;NY!).

Potentilla wardii Greene Leafl. Bot. Obs. & Crit. 2: 138. 1911. Rosaceae. = *P. hippiana* Lehm. Wayne Co., Thousand Lake Mt., Ward sn, 1875 (US!).

Primula incana Jones Proc. Calif. Acad. II, 5: 705. 1895. Primulaceae. Garfield Co., Sevier River, Jones 5312av, 1894 (POM!).

Primula maguirei **L.O. Williams** Amer. Midl. Naturalist 7: 747. 1936. Primulaceae. Cache Co., Logan Canyon, Maguire & Maguire 3650, 1932 (M0;UT!;UTC!).

Primula specuicola **Rydb.** Bull. Torrey Bot. Club 40: 461. 1913. Primulaceae. San Juan Co., near Bluff, Rydberg 9882, 1911 (NY!;US!;UT!).

Prosartes trachycarpa Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 344. 1871. Liliaceae. = *Disporum trachycarpum* Wats. Summit Co., Parleys Park, Watson 1166,1869 (NY!).

Psathyrotes pilifera Gray Proc. Amer. Acad. 19: 50. 1883. Asteraceae. Kane Co., Kanab, Thompson sn, 1872 (GH).

Pseudocymopterus tidestromii **Coult. & Rose** Contr. U.S. Natl. Herb. 12: 447. 1909. Apiaceae. = *Cymopterus lemmonii* (Coult. & Rose) Dorn Sevier Co., Mt. Terrell, Tidestrom 1811, 1908 (US!).

Pseudocymopterus versicolor **Rydb.** Fl. Rocky Mts. 623, 1064. 1917. Apiaceae. = *Cymopterus lemmonii* (Coult. & Rose) Dorn Garfield Co., Aquarius Plateau, Rydberg & Carlton 7426, 1905 (NY!).

Pseudopteryxia longiloba **Rydb.** Bull. Torrey Bot. Club 40: 72. 1913. Apiaceae. = *Cymopterus hendersonii* (Coult. & Rose) Cronq. San Juan Co., Abajo Mts., Rydberg & Garrett 9761, 1911 (NY!;UT!).

Pseudotsuga globosa **Flous** Bull. Soc. Hist. Nat. Toulouse 66: 334. 1934. Pinaceae. = *P. menziesii* (Mirb.) Franco Salt Lake Co., Big Cottonwood Canyon, Rydberg & Carlton 6587, 1905 (?).

Psoralea castorea Wats. Proc. Amer. Acad. 14: 291. 1879. Fabaceae. Beaver Co. (more likely Beaverdam, Arizona), near Beaver City, Palmer 96, 1877 (US!;NY!;BRY!;ISC!).

Psoralea epipsila Barneby Leafl. W. Bot. 3: 193. 1943. Fabaceae. Kane Co., 17 mi e Kanab, Ripley & Barneby 4832, 1942 (CAS!).

Psoralea juncea Eastw. Proc. Calif. Acad. II, 6: 286. 1897. Fabaceae. San Juan Co., Epsom Creek, Eastwood 21, 1895 (CAS!;US!;NY!).

Psoralea mephitica Wats. Proc. Amer. Acad. 14: 291. 1879. Fabaceae. Washington Co., near St. George, Palmer 97, 1877 (US!;NY!;BRY!;ISC!).

Psoralea pariensis **Welsh & Atwood in Welsh, Atwood, & Reveal** Great Basin Naturalist 35: 353. 1975. Fabaceae. Garfield Co., Bryce Canyon, Welsh & Murdock 12859, 1975 (BRY!;UT!;NY!;US!;UTC!;ISC!).

Psoralea rafaelensis Jones Contr. W. Bot. 18: 41. 1933. Fabaceae. = *P. aromatica* Payson Grand Co., LaSal Mts., Jones sn, 1914 (US!;CAS!).

Psoralea rafaelensis Jones var. ***magna*** Jones Contr. W. Bot. 18: 41. 1933. Fabaceae. = *P. aromatica* Payson Emery Co., San Rafael Swell, Jones sn, 1914 (CAS!).

Psoralea stenophylla **Rydb.** Bull. Torrey Bot. Club 40: 46. 1913. Fabaceae. = *P. lanceolata* var. *stenophylla* (Rydb.) Toft & Welsh Grand Co., Wilson Mesa, Rydberg & Garrett 8367, 1911 (NY!).

Psoralea stenostachys **Rydb.** Bull. Torrey Bot. Club 40: 46. 1913. Fabaceae. = *P. lanceolata* var. *stenostachys* (Rydb.) Welsh Tooele Co., Government Well, Jones 6221, 1900 (NY!;US!;CAS!;POM!;RM!;BRY!).

Ptelea neglecta **Greene** Contr. U.S. Natl. Herb. 10: 71. 1906. Rutaceae. = *P. trifoliata* ssp. *pallida* var. *lutescens* (Greene) V.K. Bailey Kane Co., near Kanab, Wetherill sn, 1897 (CAS!).

Pterchiton occidentale **Torr. & Frem. in Frem.** Rep. Exped. Rocky Mts. 318. 1845. Chenopodiaceae. = *Atriplex canescens* (Pursh) Nutt. Davis (?) Co., Great Salt Lake, Fremont sn, 1843 (NY!).

Ptilocalais macrolepis **Rydb.** Bull. Torrey Bot. Club 38: 11. 1911. Asteraceae. = *Microseris nutans* (Geyer) Schulz-bip Salt Lake Co., Salt Lake City, Garrett 182, 1903 (US!;NY!;BRY!).

Pyrrocoma cheiranthifolia **Greene** Leafl. Bot. Obs. & Crit. 2: 47. 1910. Asteraceae. = *Haplopappus clementis* (Rydb.) Blake Sanpete Co., w. Ephriam, Tidestrom 534, 1907 (US!).

Pyrrocoma lapathifolia **Greene** Leafl. Bot. Obs. & Crit. 2: 13. 1909. Asteraceae. = *Haplopappus integrifolius* Gray? Utah, Ward 596, 1875 (US!).

Pyrrocoma subcaesia **Greene** Leafl. Bot. Obs. & Crit. 2: 12. 1909. Asteraceae. = *Haplopappus clementis* (Rydb.) Blake Aarfield Co., Panguitch Lake, Jones 6005, 1894 (US!;RM!;POM!;NY!;BRY!).

Quercus eastwoodiae **Rydb.** Bull. New York Bot. Gard. 2: 210. 1901. Fagaceae. = *Q. gambelii* Nutt. San Juan Co., Butler Wash, Eastwood 141, 1895 (NY!;US!).

Quercus stellata var. ***utahensis*** **A. DC.** Prodr. 16(2): 22. 1864. . = *Q. gambelii* Nutt. Utah? (between Salt Lake and Sierras) Beckwith (?) sn, 1854?(G).

Ranunculus acriformis **Gray** var. ***aestivalis*** **L. Benson** Amer. Midl. Naturalist 40: 43. 1948. Ranunculaceae. Garfield Co., 8.3 mi n Panguitch, Benson 13421, 1948 (POM;RM;BRY!;UT!;UTC!).

Ranunculus alismaefolius **Geyer ex Benth.** var. ***montanus*** **Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 7. 1871. Ranunculaceae. Summit (?) Co., Uinta Mts., Watson 18, 1969 (US!).

Ranunculus andersonii **Gray** var. ***tenellus*** **Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 7. 1871. Ranunculaceae. = *R. juniperinus* Jones Salt Lake (?) Co., Pilot Rock Point, Salt Lake, Watson 17, 1869 (?).

Ranunculus juniperinus **Jones** Proc. Calif. Acad. II, 5: 616. 1895. Ranunculaceae. Syn: *R. andersonii* var. *tenellus* Wats. Washington Co., 18 mi w St. George, Jones 5011, 1894 (US!).

Ranunculus multifidus **Pursh** var. ***repens*** **Hook. in Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 8. 1871. . = *R. gmelinii* var. *hookeri* (D. Don) L. Benson Summit Co., Weber Valley, Watson 24, 1869 (US!).

Ranunculus orthrorhynchus **Hook.** var. ***alpinus*** **Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 9. 1871. Ranunculaceae. = *R. adoneus* var. *alpinus* (Wats.) L. Benson Salt Lake (?) Co., Wasatch Mts., Watson 30, 1869 (US!).

Ranunculus orthrorhynchus **Hook.** var. ***platyphyllus*** **Gray** Proc. Amer. Acad. 21: 377. 1886. Ranunculaceae. Salt Lake (?) Co., Wasatch Mts., Watson 28, 1869 (US!).

Ranunculus utahensis **Rydb.** Bull. Torrey Bot. Club 29: 158. 1902. Ranunculaceae. = *R. inamoenus* var. *alpeophilus* (A. Nels.) L. Benson Salt Lake Co., Alta, Jones 1130, 1879 (NY!;POM!;UTC!).

Rhus nitens **Greene** Proc. Washington Acad. Sci. 8: 190. 1906. Anacardiaceae. = *R. glabra* L. Utah Co., Provo, Jones 5612, 1894 (US!;RM!;NY!).

Rhus utahensis **Goodding** Bot. Gaz. 37: 57. 1904. Anacardiaceae. = *R. trilobata* var. *simplicifolia* (Greene) Barkley Washington Co., Diamond Valley, Goodding 832, 1902 (US!;RM!).

Rhysopterus jonesii **Coult. & Rose** Contr. U.S. Natl. Herb. 7: 186. 1900. Apiaceae. = *Cymopterus coulteri* (Jones) Mathias Juab Co., Juab, Jones 1691, 1880 (US!;POM!;BRY!).

Ribes lacustre **(Pers.) Poir. in Lam. var.** ***lentum*** **Jones** Proc. Calif. Acad. 11, 5: 681. 1895. Saxifragaceae. = *R. montigenum* McClatchie Garfield Co., Henry Mts., Jones 5695o, 1894 (POM!).

Riddellia tagetina **var.** ***sparsiflora*** **Gray** Syn. Fl. N. Amer. 1(2): 318. 1884. Asteraceae. = *Psilostrophe sparsiflora* (Gray) A. Nels. Kane Co., (Southern Utah), Bishop, Mrs. Thompson sn, 1872 (GH?).

Rorippa integra **Rydb.** Bull. Torrey Bot. Club 29: 236. 1902. Brassicaceae. = *R. curvipes* var. *integra* (Rydb.) Stuckey Wasatch Mts., Watson 64, 1869 (US!;NY!).

Rosa chrysocarpa **Rydb.** Bull. Torrey Bot. Club 44: 74. 1917. Rosaceae. = *R. woodsii* Lindl. San Juan Co., Allen Canyon, sw of Abajo Mts., Rydberg & Garrett 9312, 1913 (NY!).

Rosa puberulenta **Rydb.** Fl. Rocky Mts. 443. 1917. Rosaceae. = *R. woodsii* Lindl. San Juan Co., Montezuma Canyon, e of Monticello, Rydberg & Garrett 9705, 1913 (NY!).

Rumex maritimus **L. var.** ***athrix*** **St.John** Rhodora 17: 79. 1915. Polygonaceae. = *R. maritimus* L. Sevier Co., Vermillion, Jones 5839, 1894 (MO;GH;POM!).

Rumex subalpina **Jones** Proc. Calif. Acad. II, 5: 720. 1895. Polygonaceae. = *R. pycnanthus* Rech. f. Piute Co., Brigham Peak, Jones 5957, 1894 (POM!; US!;RM!;BRY!;NY!).

Rumex utahensis **Rech.** f. Repert. Sp. Nov. 40: 298. 1936. Polygonaceae. = *R. salicifolius* Wein. Carbon Co., Kyune, Jones 5603, 1894 (US!).

Salicornia utahensis **Tidestr.** Proc. Biol. Soc. Washington 26: 13. 1913. Chenopodiaceae. = *S. pacifica* var. *utahensis* (Tidestr.) Munz Utah (?).

Salix lutea **Nutt. var.** ***platyphylla*** **Ball** Bot. Gaz. 71: 430. 1921. Salicaceae. = *S. rigida* Muhl. Salt Lake Co., City Creek Canyon, Ball 1336, 1908 (US!).

Saxifraga caespitosa **L. ssp.** ***exaratoides*** **var.** ***purpusii*** **Engler & Irmsch.** Pflanzenr. 4. Fam. 117(1): 377. 1916. Saxifragaceae. = *S. caespitosa* var. *minima* Blankinship Grand (?) Co., LaSal Mts., Purpus 6642, 1899 (RM!).

Schmaltzia affinis **Greene** Leafl. Bot. Obs. & Crit. 1: 135. 1905. Anacardiaceae. = *Rhus trilobala* var. *simplicifolia* (Greene) Barkeley Kane Co., Kanab, Jones 5286e, 1894 (POM!;US!).

Schoencrambe pinnata **Greene** Pittonia 3: 127. 1896. Brassicaceae. = *S. linifolia* (Nutt.) Greene Utah, Ward 1875 (US!).

Sclerocactus contorus **Heil** Cact. Succ. J. (U.S.) 51: 25. 1979. Cactaceae. San Juan Co., Canyonlands National Park, Heil sn, (UNM).

Sclerocactus parviflorus **Clover & Jotter** Bull. Torrey Bot. Club 68: 419. 1941. Cactaceae. Syn: *S. whipplei* authors, not (Engelm. & Bigel) Britt. San Juan Co., Glen Canyon, Clover & Jotter 2398, 1940 (US!).

Sclerocactus terrae-canyonae **Heil** Cact. Succ. J. (U.S.) 51: 26. 1979. Cactaceae. San Juan Co., without locality, Heil sn, (UNM).

Sclerocactus wrightiae **L. Benson** Cact. & Succ. J. (U.S.) 38: 55. 1966. Cactaceae. Emery Co., San Rafael Ridge, Benson & Benson 16595 (POM).

Scrophularia utahensis **Gandg.** Bull. Soc. Bot. France 66: 219. 1919. Scrophulariaceae. = *S. lanceolata* Pursh? Cache Co., Linford sn, 1897 (?).

Sedum meehanii **Gray** Proc. Amer. Acad. 16: 105. 1880. Crassulaceae. = ? *S. lanceolatum* Torr. Salt Lake Co., City Creek Canyon, Reading (GH).

Selaginella utahensis **Flowers** Amer. Fern J. 39: 83. 1949. Selaginellaceae. Washington Co., s St. George, Cottam 5644, 1931 (UT!;BRY!).

Selaginella watsonii **Underwood** Bull. Torrey Bot. Club 25: 127. 1898. Selaginellaceae. Salt Lake Co., Cottonwood Canyon, Watson 2370, 1869 (US!).

Senecio aquariensis **Greenm.** Ann. Missouri Bot. Gard. 3: 144. 1916. Asteraceae. = *S. streptanthifolius* Greene Garfield Co., Aquarius Plateau, Ward 505, 1875 (GH;US!).

Senecio convallium **Greenm.** Ann. Missouri Bot. Gard. 1: 266. 1914. Asteraceae. = *S. canus* Hooker Wayne Co., Rabbit Valley, Ward 704, 1875 (US!).

Senecio dimorphophyllus **Greene var.** ***intermedius*** **T.M. Barkley** Trans. Kansas Acad. 65: 362. 1963. Asteraceae. San Juan Co., LaSal Mts., Payson & Payson 4097, 1924 (MO;GH;RM!;UC).

Senecio incurvus **A. Nels.** Univ. Wyoming Publ. Bot. 1: 141. 1926. Asteraceae. = *S. spartioides* T. & G. Washington Co., Zion National Park, Nelson 9988, 1922 (RM!).

Senecio jonesii **Rydb.** Bull. Torrey Bot. Club 27: 179. 1900. Asteraceae. = *S. streptanthifolius* Greene Salt Lake Co., Alta, Jones 1125, 1879 (NY!;POM!;UTC!).

Senecio kingii **Rydb.** Bull. Torrey Bot. Club 37: 468. 1910. Asteraceae. = *S. eremophilus* var. *kingii* (Rydb.) Greenm. Salt Lake Co., Cottowood Canyon, Watson 676 (NY!;US!).

Senecio lapidum **Greenm.** Ann. Missouri Bot. Gard. 4: 18. 1917. Asteraceae. = *S. multilobatus* T. & G. ex Gray Washington Co., Silver Reef, Jones 5163v, 1894 (NY!;BRY!).

Senecio leonardii **Rydb.** Bull. Torrey Bot. Club 37: 468. 1910. Asteraceae. = *S. streptanthifolius* Greene Utah Co., American Fork Canyon, Leonard 143, 1884 (NY!).

Senecio lugens **Richards var.** ***hookeri*** **D.C. Eaton** in Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 188. 1871. Asteraceae. = *S. sphaerocephalus* Greene Summit Co., Salt Lake City to Uintas, Watson 661, 1869 (US!;NY!).

Senecio malmstenii **Blake in Tidestr.** Proc. Biol. Soc. Washington 36: 183. 1923. Asteraceae. = *S. streptanthifolius* Greene Kane Co., Little Podunk Creek, Malmsten 131, 1916 (US!).

Senecio multilobatus **T. & G. ex Gray** Mem. Amer. Acad. II, 4: 109. 1849. Asteraceae. Uintah Co., Uinta River, Fremont 549, 1845 (NY!).

Senecio pammelii Greenm. Ann. Missouri Bot. Gard. 3: 118. 1916. Asteraceae. = S. *streptanthifolius* Greene Morgan Co., Peterson, Pammel & Blackwood 3870, 1902 (MO;GH).

***Senecio platylobus* Rydb.** Bull. Torrey Bot. Club 27: 181. 1900. Asteraceae. = S. *streptanthifolius* Greene Wasatch Mountains, Watson 671, 1869 (NY!).

***Senecio rubricaulis* var. *aphanactis* Greenm.** Ann. Missouri Bot. Gard. 3: 174. 1916. Asteraceae. = S. *streptanthifolius* Greene Cache Co., Logan, Smith 2208, 1910 (UTC!).

***Senecio wardii* Greene** Pittonia 4: 116. 1900. Asteraceae. = S. *streptanthifolius* Greene Sevier Co., Fish Lake Mt., Ward 332, 1875 (GH;US!).

***Shepherdia rotundifolia* Parry** Amer. Naturalist 9: 350. 1875. Elaeagnaceae. Kane Co., Valley of the Virgin, Siler sn, 1875 (US!;NDG!).

***Sidalcea crenulata* A. Nels.** Proc. Biol. Soc. Washington 17: 93. 1904. Malvaceae. = S. *neomexicana* var. *crenulata* (A. Nels.) C.L. Hitchc. Juab Co., Juab, Goodding 1091, 1902 (RM!;BRY!;NY!;ISC!).

***Sieversia scapoidea* A. Nels. in Coult. & Nels.** New Man. Bot. Rocky Mts. 263. 1909. Rosaceae. = *Geum rossii* (R. Br.) Ser. Piute Co., w of Marysvale, Jones 5871, 1894 (RM!;POM!).

***Silene petersonii* Maguire var *minor* Hitchc. & Maguire** Univ. Washington Publ. Biol. 13: 38. 1947. Caryophyllaceae. Garfield Co., Red Canyon, Maguire 19550, 1940 (UTC!;NY!).

Silene petersonii* Maguire var. *petersonii Madroño 6: 24. 1941. Caryophyllaceae. Sanpete Co., Wasatch Plateau, Maguire 20000, 1940 (UTC!;NY!;BRY!).

***Sisyrinchium radicatum* Bickn.** Bull. Torrey Bot. Club. 28: 576. 1901. Iridaceae. = S. *demissum* Greene Washington Co., St. George, Palmer 456, 1877 (NY!;ISC!).

***Sitanion insulare* J.G. Sm.** USDA Div. Agrostol. Bull. 18: 14. 1899. Poaceae. = *Agrositanion saxicola* (Scribn. & Sm.)Bowden Tooele Co., Carrington Island, Watson 1338, 1869 (US!).

***Solidago garrettii* Rydb.** Bull. Torrey Bot. Club 37: 134. 1910. Asteraceae. = S. *sparsiflora* Gray Salt Lake Co., Big Cottonwood Canyon, Garrett 2041, 1906 (NY!;UT!).

***Solidago radulina* Rydb.** Bull. Torrey Bot. Club 31: 650. 1904. Asteraceae. = S. *nana* Nutt. Salt Lake Co., Cottonwood Canyon, Watson 558, 1869 (NY).

***Sonchus asper* (L.) All. var. *glanduliferus* Garrett** Spr. Fl. Wasatch ed. 3. 119. 1917. Asteraceae. = S. *asper* (L.) Hill Utah (?).

***Sophia leptostylis* Rydb.** Bull. Torrey Bot. Club 39: 325. 1912. Brassicaceae. = *Descurainia californica* (Gray) Schulz Salt Lake Co., Big Cottonwood Canyon, Rydberg & Carlton 6629, 1905 (NY!;US!;RM!).

***Sphaeralcea caespitosa* Jones** Contr. W. Bot. 12: 4. 1908. Malvaceae. Beaver (?) Co., Wah Wah, Jones sn, 1906 (POM!;CAS!;US!;BRY!;NY!).

Sphaeralcea grossulariifolia* (H. & A.) Rydb. var. *moorei Welsh Great Basin Naturalist 40: 35. 1980. Malvaceae. Kane Co., Lake Powell, Welsh & Atwood 11597, 1972 (BRY!).

Sphaeralcea leptophylla* (Gray) Rydb. var. *janeae Welsh Great Basin Naturalist 40: 36. 1980. Malvaceae. San Juan Co., White Rim road, Welsh 7085, 1968 (BRY!).

***Sphaeralcea psoraloides* Welsh** Great Basin Naturalist 40: 36. 1980. Malvaceae. Wayne Co., Salt Wash, Welsh 13348, 1977 (BRY!).

***Sphaeralcea subrhomboidea* Rydb.** Bull. Torrey Bot. Club 40: 59. 1913. Malvaceae. = S. *munroana* (Dougl.) Spach Wasatch Co., Midway, Carlton & Garrett 6691, 1905 (NY!;US!).

***Sphaeromeria ruthiae* Holmgren, Schultz, & Lowrey** Brittonia 28: 257. 1976. Asteraceae. Washington Co., Zion Canyon, Holmgren et al. 16603, 1974 (UTC!; BRY!;UT!;US!;NY!).

***Sphaerostigma utahense* Small** Bull. Torrey Bot. Club 23: 191. 1896. Onagraceae. = *Camissonia boothii* ssp. *alyssoides* (H. & A.) Raven Beaver Co., Milford, Jones 1773, 1880 (NY!;POM!).

***Spiraea caespitosa* Nutt. in T. & G. var. *elatior* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 81. 1871. Rosaceae. = *Petrophytum caespitosum* (Nutt.) Rydb. Box Elder Co., Raft R. Mts., Watson 307, 1869 (NY!).

***Stachys asperrima* Rydb.** Bull. Torrey Bot. Club 36: 682. 1909. Lamiaceae. = S. *palustris* L. Salt Lake Co., Jordan, Leonard 138, 1884 (NY!).

***Stanleya canescens* Rydb.** Bull. Torrey Bot. Club 29(1): 232. 1902. Brassicaceae. = S. *pinnata* var. *pinnata* Beaver Co., Frisco, Jones 1809, 1880 (NY!;POM!).

***Stenotus falcatus* Rydb.** Bull. Torrey Bot. Club 27: 616. 1900. Asteraceae. = *Haplopappus acaulis* var. *glabratus* (D.C. Eaton) Hall Washington Co. (s. Utah), Red Creek, Palmer 202, 1877 (US!;NY!;ISC!).

***Stenotus latifolius* A. Nels.** Bot. Gaz. 37: 266. 1904. Asteraceae. = *Haplopappus acaulis* var. *glabratus* (D.C. Eaton) H.M. Hall Utah Co., near Provo, Goodding 1111, 1902 (US!;NY!;BRY!;ISC!).

***Stipa arida* Jones** Proc. Calif. Acad. II, 5: 725. 1895. Poaceae. Syn: S. *mormonum* Mez Piute Co., near Marysvale, Jones 5377, 1894 (POM!;RM!;US!;NY!).

***Stipa mormonum* Mez.** Feddes Repert. 17: 209. 1921. Poaceae. = S. *arida* Jones Beaver Co., Milford, Jones 2106, 1880 (US!frag;UT!;UTC!).

***Stipa parishii* var. *depauperata* Jones** Contr. W. Bot. 14: 11. 1912. Poaceae. = S. *coronata* var. *depauperata* (Jones) A.S. Hitchc. Juab Co., Detroit, Jones, 1891 (US!).

***Stipa pinetorum* Jones** Proc. Calif. Acad. II, 5: 724. 1895. Poaceae. Garfield Co., Panguitch Lake, Jones 6023, 1894 (POM!;US!).

***Streptanthus crassicaulis* Torr. in Stansbury** Expl. Great Salt Lake, Append. D. Botany 383. 1852. Brassicaceae. = *Caulanthus crassicaulis* (Torr.) Wats. Tooele Co., w shore of Great Salt Lake, Stansbury sn, 1850 (NY!).

***Suaeda intermedia* Wats.** Proc. Amer. Acad. 14: 296. 1879. Chenopodiaceae. Sevier Co., Glenwood, Ward 718, 1875 (US!).

***Swertia fritillaria* Rydb.** Bull. Torrey Bot. Club 40: 465. 1913. Gentianaceae. = S. *perennis* L. Salt Lake Co, Big Cottonwood Canyon, Garrett 1566, 1905 (NY!;UT!).

***Synthris laciniata* (Gray) Rydb. ssp. *ibahpensis* Pennell** Proc. Acad. Nat. Sci. Philadelphia 85: 92. 1933. Scrophulariaceae. = S. *laciniata* (Gray) Rydb. Juab Co., Mt. Ibapah, Stanton 1000, 1932 (PH).

***Synthris pinnatifida* Wats.** Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 227. 1871. Scrophulariaceae. Utah Co., American Fork Canyon, Watson 802, 1869 (US!;NY!).

Synthris pinnatifida Wats. var. ***laciniata*** Gray Syn. Fl. N. Amer. 2(1): 286. 1878. Scrophulariaceae. = S. *laciniata* (Gray) Sevier Co., Fish Lake Mts., Ward 327, 1875 (US!).

Tanacetum diversifolium D.C. Eaton Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 180. 1871. Asteraceae. = *Sphaeromeria diversifolia* Rydb. Utah Co., American Fork Canyon, Watson 632, 1869 (US!).

Tetradymia linearis Rydb. Bull. Torrey Bot. Club 32: 130. 1905. Asteraceae. = *T. canescens* DC. Iron Co., Rock Creek, Palmer 264, 1877 (NY!).

Tetradymia spinosa H. & A. var. ***longispina*** Jones Proc. Calif. Acad. II, 5: 698. 1895. Asteraceae. = *T. axillaris* var. *longispina* Jones Washington Co., St. George, Jones 5110, 1894 (POM!;US!;NY!;BRY!).

Tetraneuris epunctata A. Nels. Bot. Gaz. 37: 275. 1904. Asteraceae. = *Hymenoxys acaulis* var. *caespitosus* (A. Nels.) Parker Uintah Co., Dyer Mine, Goodding 1236, 1902 (RM!;US!;UT!;NY!;BRY!;ISC!).

Thalictrum duriusculum Greene Leafl. Bot. Obs. & Crit. 2: 92. 1910. Ranunculaceae. = *T. alpinum* L. Sevier Co., near Fish Lake, Jones 5826a, 1894 (US!;POM!).

Thelesperma subnudum Gray Proc. Amer. Acad. 10: 72. 1874. Asteraceae. Washington Co., near St. George, Parry 109, 1874 (US!;NY!;ISC!;BRY!).

Thelypodiopsis argillacea Welsh & Atwood Great Basin Naturalist 37: 95. 1977 Brassicaceae. Uintah Co., Big Pack Mountain, Atwood 6627, 1976 (BRY!).

Thelypodiopsis barnebyi Welsh & Atwood in Welsh Brittonia 33: 300. 1981. Brassicaceae. Emery Co., San Rafael Swell, Welsh 20345, 1981 (BRY!;NY!;GH!;UTC!).

Thelypodium elegans Jones Zoe 4: 265. 1893. Brassicaceae. = *Thelypodiopsis elegans* (Jones) Rydb. Grand Co., Westwater, Jones sn, 1891 (POM!;RM!;BRY!;NY!).

Thelypodium macropetalum Rydb. Bull. Torrey Bot. Club 29: 233. 1902. Brassicaceae. = *T. sagittatum* var. *sagittatum* Davis Co., Farmington, Jones 1841, 1881 (NY!;US!;CAS!;POM!;BRY!;UTC!).

Thelypodium ovalifolium Rydb. Bull. Torrey Bot. Club 30: 253. 1903. Brassicaceae. = *T. sagittatum* var. *ovalifolium* (Rydb.) Welsh & Reveal Garfield Co., Panguitch Lake, Jones 6015e, 1894 (US!;POM!;NY!).

Thelypodium palmeri Rydb. Bull. Torrey Bot. Club 34: 433. 1907. Brassicaceae. = *T. sagittatum* var. *ovalifolium* (Rydb.) Welsh & Reveal Washington Co., (s. Utah), Palmer 25, 1877 (NY!;US!;BRY!;ISC!).

Thelypodium rollinsii Al-Shehbaz Contr. Gray Herb. II, 204: 97. 1973. Brassicaceae. Juab Co., 12 mi n Scipio, I. & N. Al- Shehbaz 6913, 1969 (GH).

Thelypodium sagittatum (Nutt.) Endl. var. ***vermicularis*** Welsh & Reveal Great Basin Naturalist 37: 358. 1978. Brassicaceae. Sevier Co., 4 mi se Sigurd, Welsh & Atwood 11718, 1972 (BRY!).

Thelypodium suffrutescens Rollins in Graham Ann. Carnegie Mus. 26: 224. 1937. Brassicaceae. = *Glaucocarpum suffrutescens* (Rollins) Rollins Uintah Co., Big Pack Mtn, Graham 8959, 1935 (GH;CM!;NY!).

Thelypodium utahense Rydb. Bull. Torrey Bot. Club 29: 233. 1902. Brassicaceae. = *Caulanthus lasiophyllus* var. *utahensis* (Rydb.) Jeps. Washington Co., St. George, Jones 1648, 1880 (US!;UT!;POM!;NY!).

Thelypodium wrightii Gray var. ***tenellum*** Jones Proc. Calif. Acad. II, 5: 622. 1895. Brassicaceae. = *T. laxiflorum* Al-Shehbaz Utah Co., Slate Canyon, Jones 5559, 1894 (POM!;US!;CAS!;RM!;NY!).

Thlaspi fendleri Gray var. ***tenuipes*** Maguire Amer. Midl. Naturalist 24: 469. 1942. Brassicaceae. = *T. montanum* var. *montanum* Sanpete Co., Mayfield Canyon, Maguire 19998, 1940 (UTC!).

Thlaspi prolixum A. Nels. Amer. J. Bot. 32: 287. 1945. Brassicaceae. = *T. montanum* var. *montanum* Piute Co., Marysvale, Jones 5374, 1894 (RM!;POM!).

Thysanocarpus trichocarpus Rydb. Bull. Torrey Bot. Club 30: 253. 1903. Brassicaceae. = *T. curvipes* Hook. Washington Co., Silver Reef, Jones 5163b, 1894 (US!).

Tithonia argophylla D.C. Eaton Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 423. 1871. Asteraceae. = *Enceliopsis argophylla* (D.C. Eaton) A. Nels. Washington Co., St. George, Palmer sn, 1877 (US!).

Townsendia annua Beaman Contr. Gray Herb. II, 183. 132. 1957. Asteraceae. San Juan Co., 1.5 mi n. Bluff, Maguire 13509, 1936 (UTC!).

Townsendia aprica Welsh & Reveal Brittonia 20: 375. 1968. Asteraceae. Sevier Co., s Fremont Jct., Reveal & Welsh 721, 1966 (BRY!;CAS!).

Townsendia dejecta A. Nels. Bot. Gaz. 37: 267. 1904. Asteraceae. = *T. montana* var. *montana* Uintah Co., Dyer Mine, Goodding 1283, 1902 (US!;RM!).

Townsendia florifer (Hook.) Gray var. ***communis*** Jones Proc. Calif. Acad. II, 5: 697. 1895. Asteraceae. = *T. florifer* (Hook.) Gray Piute Co., Kingston, Jones 5322f, 1894 (POM!;US!;BRY!).

Townsendia incana Nutt. var. ***prolixa*** Jones Contr. W. Bot. 13: 15. 1910. Asteraceae. = *T. strigosa* Nutt. Duchesne Co., Duchesne Valley, Jones 5323, 1908 (POM!;BRY!).

Townsendia mensana Jones Contr. W. Bot. 13: 15. 1910. Asteraceae. Duchesne Co., near Theodore, Jones sn, 1908 (POM!;BRY!).

Townsendia mensana Jones var. ***jonesii*** Beaman Contr. Gray Herb. II, 183: 88. 1957. Asteraceae. = *T. jonesii* (Beaman) Reveal Juab Co., Mammoth, Jones sn, 1910 (POM!;BRY!).

Townsendia minima Eastw. Leafl. W. Bot. 1: 206. 1936. Asteraceae. Garfield Co., Bryce Cyn., Eastwood & Howell 727, 1933 (CAS!).

Townsendia montana Jones Zoe 4: 262. 1893. Asteraceae. Syn: *T. dejecta* A. Nels. Salt Lake Co., Alta, above Flagstaff Mine, Jones sn, 1879 (POM!).

Townsendia scapigera var. ***ambigua*** Gray Proc. Amer. Acad. 16: 84. 1880. Asteraceae. = *T. florifer* (Hook.) Gray Wayne Co., Rabbit Valley, Ward 523, 1875 (US!).

Townsendia watsonii Gray Proc. Amer. Acad. 16: 84. 1880. Asteraceae. = *T. florifer* (Hook.) Gray Tooele Co., Stansbury Island, Watson 520, 1869 (US!).

Toxicodendron longipes Greene Leafl. Bot. Obs. & Crit. 1: 118. 1905. Anacardiaceae. = *T. rydbergii* (Small) Greene Sevier Co., s Glenwood, Ward 212, 1875 (US!).

Trifolium andersonii Gray var. ***friscanum*** Welsh Great Basin Naturalist 38: 355. 1978. Fabaceae. Beaver Co., Grampian Hill, Peabody et al 406, 1976 (BRY!;NY!).

Trifolium confusum Rydb. Bull. Torrey Bot. Club 34: 46. 1907. Fabaceae. = *T. longipes* var. *pygmaeum* Gray Iron Co., near Cedar City, Parry 35, 1874 (NY!).

Trifolium inequale Rydb. Bull. Torrey Bot. Club 34: 47. 1907. Fabaceae. = *T. parryi* var. *montanense* (Rydb.) Welsh Summit Co., Bear River Canyon, Watson 243, 1869 (NY!).

Trifolium kingii Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 59. 1871. Fabaceae. Summit Co., Parleys Park, Watson 239, 1869 (US!;NY!).

Trifolium longipes Nutt. var. ***brachypus*** Wats. Biblio. Index N. Amer. Bot. 264. 1878. Fabaceae. = *T. longipes* var. *pygmaeum* Gray Washington Co., near St. George, Palmer sn, 1870 (GH).

Trifolium macilentum Greene Pittonia 3: 223. 1897. Fabaceae. Washington Co., (s. Utah), Palmer sn, 1877 (US!;NY!).

Trifolium uintense Rydb. Bull. Torrey Bot. Club 34: 47. 1907. Fabaceae. = *T. dasyphyllum* var. *uintense* (Rydb.) Welsh Summit Co., Uintas, Watson 241, 1869 (NY!;US!).

Trifolium villiferum House Bot. Gaz. 41: 335. 1906. Fabaceae. = *T. eriocephalum* var. *villiferum* (House) Martin Washington Co., (s. Utah), Palmer 91, 1877 (US!;NY!;BRY!).

Triglochin maritima L. var. ***debile*** Jones Proc. Calif. Acad. II, 5: 722. 1895. Juncaginaceae. = *T. concinna* var. *debile* (Jones) Howell Kane Co., Johnson, Jones 5289, 1894 (US!;POM!).

Valeriana puberulenta Rydb. Bull. Torrey Bot. Club 36: 697. 1909. Valerianaceae. = *V. acutiloba* var. *pubicarpa* (Rydb.) Cronq. Piute Co., Bullion Creek, Rydberg & Carlton 7065, 1905 (NY!;US!;BRY!).

Valeriana pubicarpa Rydb. Bull. Torrey Bot. Club 36: 697. 1909. Valerianaceae. = *V. acutiloba* var. *pubicarpa* (Rydb.) Cronq. Juab Co., Mt. Nebo, Rydberg & Carlton 7717, 1905 (NY!;US!;RM!).

Valeriana utahensis Gandg. Bull. Soc. Bot. France 65: 37. 1908. Valerianaceae. = *V. acutiloba* var. *pubicarpa* (Rydb.) Cronq. Cache (?) Co., Linford sn, 1907 (?).

Verbesina scaposa Jones Zoe 2: 248. 1891. Asteraceae. = *Enceliopsis nutans* (Eastw.) A. Nels. Grand Co., Cisco, Jones sn, 1890 (POM!;BRY!).

Viguiera soliceps Barneby Leafl. W. Bot. 10: 316. 1966. Asteraceae. = *Heliomeris soliceps* (Barneby) Yates Kane Co., Cottonwood Canyon, Barneby 14435, 1966 (NY!;US!;UTC!).

Vilfa depauperata Torr. exHook. var. ***filiformis*** Thurb. in Wats. Rep. U.S. Geol. Explor. 40th Parallel, Bot. 5: 376. 1871. Poaceae. = *Muhlenbergia filiformis* (Thurb.) Rydb. Summit Co., Uinta Mts., Watson 1281, 1869 (US?).

Viola beckwithii T. & G. in Beckwith Rep. U.S. Explor. & Surv. R.R. Pacific 2: 119. 1855. Violaceae. Utah, between Salt Lake and Sierra Nevada, Beckwith sn, 1854(NY!).

Viola beckwithii T. & G. var. ***cachensis*** C.P. Sm. Muhlenbergia 7: 136. 1912. Violaceae. = *V. beckwithii* T. & G. Utah.

Viola bellidifolia Greene ssp. ***valida*** Baker Madroño 5: 223. 1940. Violaceae. = *V. adunca* J.E. Sm. Salt Lake Co., Brighton, Baker 8519, 1936 (UTC!).

Viola bonnevillensis Cottam Bull. Univ. Utah Biol. Ser. 3: 3. 1939. Violaceae. = *V. beckwithii* T. & G. Salt Lake Co., Salt Lake City, Cottam 7067, 1937 (UT!).

Viola clauseniana Baker Madroño 4: 194. 1938. Violaceae. = *V. nephrophylla* Greene Washington Co., Zion National Park, Baker 84348, 1936 (UC).

Viola mamillata Greene Leafl. Bot. Obs. & Crit. 2: 33. 1910. Violaceae. = *V. adunca* J.E. Sm. Uintah Co., Dyer Mine, Goodding 1202, 1902 (US!;RM!;UT!;BRY!).

Viola oxysepala Greene Leafl. Bot. Obs. & Crit. 2: 34. 1910. Violaceae. = *V. adunca* J.E. Sm. Sanpete Co., inter Willow & Ephriam creeks, Tidestrom 2476, 1909 (NDG!).

Viola tidestromii Greene Leafl. Bot. Obs. & Crit. 2: 234. 1910. Violaceae. = *V. adunca* J.E. Sm. Sanpete Co., Ephriam Creek, Tidestrom 1143, 1908 (NDG!).

Viola utahensis Baker & Clausen Leafl. W. Bot. 5: 145. 1949. Violaceae. = *V. purpurea* Kellogg Cache Co., Providence Canyon, Maguire 16026, 1937 (UTC; US!;NY!;UTC!).

Whipplea utahensis Wats. Amer. Naturalist 7: 300. 1873. Saxifragaceae. = *Fendlerella utahensis* (Wats.) Heller Kane Co., Kanab, Thompson 243, 1872 (US!).

Wyethia scabra Hook. var. ***attenuata*** W.A. Weber Amer. Midl. Naturalist 35: 425. 1946. Asteraceae. Kane Co., 10.5 mi n Kanab, Carter 1424, 1938 (WS).

Wyethia scabra Hook. var. ***canescens*** W.A. Weber Amer. Midl. Naturalist 35: 425. 1946. Asteraceae. San Juan Co., s Mexican Hat, Goodman & Hitchcock 1352, 1930 (CAS!;RM!;NY!).

Wyomingia vivax A. Nels. Bot. Gaz. 56: 70. 1913. Asteraceae. = *Erigeron utahensis* var. *sparsifolius* (Eastw.) Cronq. San Juan Co., Geyser Canyon, Walker 355, 1912 (US!).

Xanthocephalum petradoria Welsh & Goodrich in Welsh Brittonia 33: 301. 1981. Asteraceae. Millard Co., Canyon Mts., Goodrich 15240, 1980 (BRY!;ASU!; GH!;M0!;NY!;RM!;TEX!;UC!;US!;UT!).

Xylophacos aragaloides Rydb. Bull. Torrey Bot. Club 34: 48. 1907. Fabaceae. = *Astragalus amphioxys* var. *amphioxys* Washington Co., St. George, Jones 1633, 1880 (NY!;POM!;ISC!).

Xylophacos marianus Rydb. Bull. Torrey Bot. Club 52: 233. 1925. Fabaceae. = *Astragalus marianus* (Rydb.) Barneby Piute Co., Marysvale, Jones 5355, 1894 (NY!;US!;POM!).

Xylophacos medius Rydb. Bull. Torrey Bot. Club 52: 232. 1925. Fabaceae. = *Astragalus eurekensis* Jones Tooele Co., Lake Point, Jones 1743, 1880 (US!; CAS!;POM!;BRY!;NY!;UT!).

Xylophacos melanocalyx Rydb. Bull. Torrey Bot. Club 52: 149. 1925. Fabaceae. = *Astragalus amphioxys* var. *amphioxys* Washington Co., Beaverdam Mts., Jones 5009, 1894 (NY!).

Xylophacos uintensis Rydb. Bull. Torrey Bot. Club 32: 662. 1905. Fabaceae. = *Astragalus argophyllus* var. *argophyllus* Salt Lake Co., Salt Lake V., Jones 1633b, 1880 (POM!).

Xylorhiza cronquistii Welsh & Atwood in Welsh Brittonia 33: 302. 1981. Asteraceae. Kane Co., Horse Mt., Welsh & Welsh 12819, 1975 (BRY!).

Xylorhiza glabriuscula Nutt. var. ***linearifolia*** T.J. Watson Brittonia 29: 215. 1977. Asteraceae. Grand Co., 6 mi nw Moab, Watson 679, 1971 (TEX; COLO;GH;MP;MONTU;NY!;UC).

Xylorhiza lanceolata Rydb. Bull. Torrey Bot. Club 37: 146. 1910. Asteraceae. = *X. tortifolia* var. *tortifolia* Washington Co., St. George, Palmer 208, 1877 (NY!;US!).

Yucca angustissima **Engelm. var. *avia* Reveal** Intermountain Fl. 6: 534. 1977. Liliaceae. Piute (?) Co., Loa Pass, Jones 5639a, 1898 (US!).

Yucca harrimaniae **Trel.** Rep. Missouri Bot. Gard. 13: 59. 1902. Agavaceae. Syn: *Y. harrimaniae* var. *gilbertiana* Trel. Carbon Co., Helper, Trelease 3233, 1889 (MO!).

Yucca harrimaniae **Trel. var. *gilbertiana* Trel.** Rep. Missouri Bot. Gard. 18: 225. 1907. Agavaceae. = *Y. harrimaniae* Trel. Juab Co., Fish Springs or House Range, Gilbert sn, 1901 (US!).

Yucca kanabensis **McKelvey** Yuccas S.W. U.S. 2: 122. 1947. Agavaceae. Syn: *Y. angustissima* var. *kanabensis* (McKelvey) Reveal Kane Co., between Mt. Carmel & Kanab, Mckelvey 4347a, 1934 (A).

Yucca toftiae **Welsh** Great Basin Naturalist 34: 308. 1974. Agavaceae. Syn: *Y. angustissima* var. *toftiae* (Welsh) Reveal San Juan Co., Lake Powell, Welsh 11935a, 1973 (BRY!;NY!).

Yucca utahensis **McKelvey** Yuccas S.W. U.S. 2: 94. 1947. Agavaceae. Syn: *Y. elata* var. *utahensis* (McKelvey) Reveal Washington Co., Santa Clara V., McKelvey 4167, 1934 (A).

Zauschneria garrettii **A. Nels.** Proc. Biol. Soc. Washington 20: 36. 1907. Onagraceae. = *Epilobium canum* (Greene) Raven Salt Lake Co., Big Cottonwood Canyon, Garrett 2031, 1906 (UT!).

BIBLIOGRAPHY

AL-SHEHBAZ, I. A. 1973. The biosystematics of the genus *Thelypodium* (Cruciferae). Contr. Gray Herb. 11, 204: 3–148.

ANDERSON, L. C. 1981. *Chrysothamnus nauscosus* ssp. *iridis* (Asteraceae): a new endemic from Utah. Great Basin Naturalist 41(3): 311–313.

ATWOOD, N. D. 1972. New species in the *Phacelia crenulata* group (Hydrophyllaceae). Rhodora 74: 451–463.

______. 1973. Two new species of *Phacelia* (Hydrophyllaceae). Phytologia 26: 437–438.

BAILEY, L. H. 1884. Notes on Carex–I. Bot. Gaz. 9:117–122.

BAKER, M. S. 1938. An undescribed species of *Viola* from Utah. Madrono 4: 194–196.

______. 1940. Studies in western violets–III. Madrono 5: 218–231.

BAKER, M. S. AND J. CLAUSEN. 1949. Studies in western Violets–IV. Leafl. W. Bot. 5: 141–156.

BALL, C. R. 1921. Undescribed willows of the section Cordatae. Bot. Gaz. 71: 426–437.

BARKLEY, T. M. 1962. A revision of *Senecio aureus* Linn. and allied species. Trans. Kansas Acad. Sci. 65: 318–408.

BARNEBY, R. C. 1943. Miscellaneous diagnoses. Leafl. W. Bot. 3: 193–199.

______. 1944. Alice Eastwood semi-centennial publications No. 3. Pugillus Astragalorum Alter. Proc. Calif. Acad. IV, 25:147–169.

______. 1945. Pugillus Astragalorum–IV: The section Diplocystium. Leafl. W. Bot. 4: 65–147.

______. 1946. Pugillus Astragalorum–V. Leafl. W. Bot. 4: 228–238.

______. 1947. Pugillus Astragalorum–VI: Notes on section Drabellae. Leafl. W. Bot. 5: 1–9.

______. 1947. Pugillus Astragalorum–VII: A revision of the Argophylli. Amer. Midl. Naturalist 37: 421–451.

______. 1949. Pugillus Astragalorum–X: New species, varieties and combinations. Amer. Midl. Naturalist 41: 496.

______. 1949. *Eriogonum villiflorum* and its near relatives in the Great Basin. Leafl. W. Bot. 5: 151–154.

______. 1952. A revision of the North American species of *Oxytropis*. DC. Proc. Calif. Acad. IV, 27: 177–312.

______. 1953. Pugillus Astragalorum–XV: Four new species. Leafl. W. Bot. 7: 31–37.

______. 1954. Pugillus Astragalorum–XVI: Minor novelties from Nevada. Leafl. W. Bot. 7: 192–196.

______. 1956. Pugillus Astragalorum–XVII: Four new species and one variety. Leafl. W. Bot. 8: 14–23.

______. 1964. Atlas of North American *Astragalus*. Mem. N.Y. Bot. Garden 13: 1–1188.

______. 1966. New sorts of *Lesquerella*, *Euphorbia*, and *Viguiera* from Kane County, Utah. Leafl. W. Bot. 10: 313–317.

BARNEBY, R. C., AND N. H. HOLMGREN. 1979. A new species of *Lomatium* (Apiaceae) from Utah. Brittonia 31: 96–100.

BEAL, W. J. 1896. Grasses of North America. Vol. 2. New York, Henry Holt and Company.

BEAMAN, J. H. 1957. The systematics and evolution of *Townsendia* (Compositae). Contr. Gray Herb. II, 183: 1–151.

BECKWITH, E. G. 1855. Reports of explorations and surveys, to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. House Rep. Exec. Doc., Vol 2, No. 91.

BENSON, L. 1948. A treatise on the North American Ranunculi. Amer. Midl. Naturalist 40: 1–264.

______. 1966. A revision of *Sclerocactus*. Cact. & Succ. J. (Los Angeles) 38: 50–57, 100–106.

______. 1969. The cacti of the United States and Canada–new names and nomenclatural combinations–I. Cact. & Succ. J. (Los Angeles) 41: 124–28.

______. 1969. The cacti of Arizona. Ed. 3, Tucson. University of Arizona Press. 218 pp.

BENTHAM, G. 1856. *Eriogonum confertiflorum* var. *stansburyi*. Page 17 *in* A. P. de Candolle. Prodromus Systematis Naturalis Regni Vegetabilis. Vol. 14.

BICKNELL, E. P. 1901. Studies in Sisyrinchium–IX: the species of Texas and the Southwest. Bull. Torrey Bot. Club 28: 570–592.

BLAKE, S. F. 1922. New Asteraceae from Utah and Nevada. Proc. Biol. Soc. Washington 35: 173–177.

______. 1931. Nine new American Asteraceae. J. Washington Acad. Sci. 21: 325–336.

———. 1935. Five new plants of the genus *Aplopappus*. Proc. Biol. Soc. Washington 48: 169–174.

———. 1937. Eleven new Asteraceae from North and South America. J. Washington Acad. Sci. 27: 374–391.

Blauer, H. C. 1965. *Helianthus* (Compositae) in Utah. Proc. Utah Acad. 42: 241–251.

Brand, A. 1907. Polemoniaceae. Pflanzenr. 4, Fam. 250 (Heft 27): 1–203.

———. 1911. Beitrag zur Kenntnis der Hydrophyllaceae.

Brandegee, M. K. 1900. *Opuntias*. Pages 97,110,120 *in* J. A. Purpus, Die Succulenten der La Sal Mountains in Utah. Monats. Kakteenk. 10: 95–120.

Brenckle, J. F., and W. P. Cottam. 1940. A new *Polygonum* from Garfield County, Utah. Bull. Univ. Utah 30: 2–7.

Britton, N. L. 1904. Four new North American birches. Bull. Torrey Bot. Club 31: 165–166.

Britton, N. L., and J. N. Rose. 1920. Cactaceae. Vol. 1 & 4, Carnegie Inst. Washington Publ. 248. 80 pp.

Britton, N. L., and J. A. Shafer. 1908. North American Trees. New York. Henry Holt and Company. 894 pp.

Broaddus, M. J. 1935. Biographical sketch of Marcus E. Jones. Contr. W. Bot. 18: 132.

———. 1952?. VI. Anna Elizabeth (Richardson) Jones, 1853–1916 (Anna). Pages 48–51 *in* A. J. Jones, Publius Virgilius and Lavinia (Burton) Jones and their family—1800–1950. Published by the family; without locality indicated.

Buchenau, F. G. P. 1890. *Juncus canadensis* var. *kuntzei*. Bot. Jahrb. 12: 272.

Candolle, A. P. de 1864. *Quercus stellata* var. *utahensis*. Prodromus Systematis naturalis Regni vegetabilis. Vol. 16. Parisiis. 160 pp.

Chamberlain, R. V. 1950. Life Sciences at the University of Utah. Background and History. Deseret News Press; Salt Lake City. 417 pp.

Chaudhri, M. N. 1968. Revision of *Paronychia*. 194.

Chuang, T. I., and L. R. Heckard. 1973. Taxonomy of *Cordylanthus* subgenus *Hemistegia* (Scrophulariaceae). Brittonia 25: 135–158.

Clover, E. U. 1938. The Cactaceae of southern Utah. Bull. Torrey Bot. Club 65: 397–412.

Clover, E. U., and L. Jotter. 1941. Cacti of the canyon of the Colorado River and tributaries. Bull. Torrey Bot. Club 68: 409–419.

Cockerell, T. D. 1904. A North American species of *Hymenoxys*. Bull. Torrey Bot. Club 31: 461–509.

Cooley, E. L. 1980. Diary of Brigham Young 1857. University of Utah Library. 105 pp.

Cottam, W. P. 1939. A new violet from Utah. Bull. Univ. Utah Biol. Ser. 4 (3). 8 pp.

Coulter, J. M. 1896. Preliminary revision of the North American species of *Echinocactus*, *Cereus* and *Opuntia*. Contr. U.S. Natl. Herb. 3: 355–462.

Coulter, J. M., and A. Nelson. 1909. New manual of botany of the central Rocky Mountains. New York. American Book Co. 646 pp.

Coulter, J. M., and J. N. Rose 1888. Revision of North American Umbelliferae. Crawfordsville. 144 pp.

———. 1900. Monograph of the North American Umbelliferae. Contr. U.S. Natl. Herb. 7: 7–256.

———. 1909. Supplement to the monograph of the North American Umbelliferae. Contr. U.S. Natl. Herb. 12: 441–451.

Coville, F. V. 1892. Descriptions of new plants from southern California, Utah and Arizona. Proc. Biol. Soc. Washington 7: 65–80.

———. 1893. Botany of the Death Valley Expedition. Contr. U.S.Natl. Herb. 4: 1–363.

Cronquist, A. 1943. The North American species of *Erigeron* centering about *E. speciosus* (Lindl.) DC. and *E. glabellus* Nutt. Bull. Torrey Bot. Club 70: 265–274.

———. 1947. Revision of the North American species of *Erigeron*, north of Mexico. Brittonia 6: 121–302.

———. 1963. Two new varieties in *Machaeranthera*. Leafl. W. Bot. 10: 11m13.

Cronquist, A., A. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. 1977. Intermountain Flora. Vol. 6. New York, Columbia Univ. Press. 584 pp.

Darlington, J. 1934. A monograph of the genus *Mentzelia*. Ann. Missouri Bot. Garden 21: 103m226.

Daston, J. S. 1946. Three noteworthy cacti of southwestern Utah. Amer. Midl. Naturalist 36: 661m662.

Dempster, L. T., and F. Ehrendorfer. 1965. Evolution of the *Galium multiflorum* complex in western North America—II. Critical taxonomic revision. Brittonia 17: 289m334.

Durand, E. M. 1860. A sketch of the botany of the basin of the Great Salt Lake of Utah. Trans. Amer. Phil. Soc. 11: 155m180.

Earle, H. W. 1980. A new *Opuntia* identified in southwestern Utah. Saguaroland Bull. 34: 15.

Eastwood, A. 1893. List of plants collected in southeastern Utah, with notes and descriptions of new species. Zoe 4: 113–127.

———. 1895. Two species of Aquilegia from the upper Sonoran zone of Colorado and Utah. Proc. Calif. Acad. II, 4: 559–562

———. 1896. Report on a collection of plants from San Juan County, in southeastern Utah. Proc. Calif. Acad. II, 6: 270–329.

———. 1903. New species of *Oreocarya*. Bull. Torrey Bot. Club 30: 238–246.

———. 1903. New species of western plants. Bull. Torrey Bot. Club 30: 483–502.

———. 1904. Some new species of western Polemoniaceae. Bot. Gaz. 37: 437–447.

———. 1927. New species of *Ceanothus*. Proc. Calif. Acad. 16: 361–363.

———. 1933. Two new species of western *Galium*. Leafl. W. Bot. 1: 55–56.

———. 1936. A new *Townsendia* from Utah. Leafl. W. Bot. 1: 206–207.

———. 1937. New species of *Dodecatheon*. Leafl. W. Bot. 2: 36–38.

———. 1937. New species of western plants. Leafl. W. Bot. 2: 54–56.

———. 1941. New species of *Castilleja*. Leafl. W. Bot. 3: 87–92.

———. 1942. New western plants IV. Leafl. W. Bot. 3: 157–160.

———. 1942. New species and varieties of *Lupinus*. Leafl. W. Bot. 3: 169–192.

Eaton, D. C. 1871. Compositae. Pages 136–208 *in* S. Watson, Botany. Report of U.S. Geological Exploration of the Fortieth Parallel. 5: Xiii–525. Washington: Government Printing Office.

______. 1875. *Notholeana parryi*. Amer. Naturalist 9: 351.

Ehrendorfer, F. 1956. Survey of the *Galium multiflorum* complex in western North America. Contr. Dudley Herb. 5: 3–21.

Engelmann, G. 1863. Additions to the cactus-flora of the territory of the United States. Trans. Acad. Sci. St. Louis 2: 199.

______. 1871. Yucca and Agave. Page 497 *in* S. Watson, Botany. Report of U.S. Geological Exploration of the Fortieth Parallel. Bot. 5: xiii–525. Washington: Government Printing Office..

______. 1878. American junipers of section Sabina. Trans. St. Louis Acad. Science 3: 588–589.

______. 1896. *Opuntia*. Pages 423–24 *in* J. M. Coulter, Preliminary revision of the North American species of *Echinocactus*, *Cereus*, and *Opuntia*. Contr. U.S. Natl. Herb. 3: 357–462.

Engler, H. G., and E. Irmscher. 1916. Saxifragaceae—*Saxifraga*. Pflanzenr. 4. Fam. 117 (Heft 67 & 69):1–707.

Ewan, J. 1950. Rocky Mountain Naturalists. The University of Denver Press. 358 pp.

Fedde, F. K. G. 1909. *Platystemon*. Pflanzenr. 4. Fam. 104. (Heft 40): 106–131.

Fedde, F. K. 1913. Neue Arten aus der Verwandtschaft der *Corydalis aurea* Willd. von Nord Amerika - VIII. Feddes Repert. 11: 497.

Flous, F. 1934. Diagnoses d' especes et varietes nouvelles de *Pseudotsuga* americains. Bull. Soc. Hist. Nat. Toulouse 66: 329–346.

Flowers, S. 1949. A new *Selaginella* from southwestern Utah. Amer. Fern J. 39: 83–86.

Fremont, J. C. 1845. Report of the exploring expedition to the Rocky Mountains in the year 1842, and to Oregon and north California in the years 1843–1844. House Rep. Doc. 199.

Gabel, M. L. 1981. The Parry herbarium. Proc. Iowa Acad. Sci. 88: 179.

Gandoger, M. 1906. Le genre *Eriogonum* (Polygonaceae). Bull. Soc. Bot. Belgium 42: 183–200.

______. 1918. Sertum plantarum novarum. Pars prima. Bull. Soc. Bot. France 65: 24–69.

______. 1919. Sertum plantarum novarum. Bull. Soc. Bot. France 66: 216–233.

______. 1920. Sertum plantarum novarum. Bull. Soc. Bot. France 66: 286–307.

Garrett, A. O. 1917. Spring flora of the Wasatch region. 3rd Ed., Lancaster Press: Salt Lake City. 144 pp.

Gates, R. R. 1915. The mutation factor in evolution, with particular reference to *Oenothera*. London, MacMillan and Co. 353 pp.

Gentry, J. L. 1974. Studies in the genus *Hackelia* (Boraginaceae) in the western United States and Mexico. Southwestern Naturalist 19: 139–146.

Goodding, L. N. 1904. Southwestern plants. Bot. Gaz. 37: 53–59.

Goodman, G. J. and C. L. Hitchcock. 1932. A new scapose *Draba* from Utah. Ann. Missouri Bot. Gard. 19: 77–78.

Gould, F. W. 1942. A systematic treatment of the genus *Camassia* Lindl. Amer. Midl. Naturalist 28: 712–742.

Graham, E. H. 1937. Botanical studies in the Uinta Basin of Utah and Colorado. Ann. Carnegie Mus. 26: 1–432.

Gray, A. 1849. Plantae Fendlerianae Novi-Mexicanae. Mem. Amer Acad. 4: 1–116.

______. 1852. Plantae Wrightianae Texano-Neo-Mexicanae. Part 1. Smithsonian Contr. Knowl. 3: 5–146.

______. 1870. Revision of the North American Polemoniaceae. Proc. Amer. Acad. 8: 247–282.

______. 1870. Miscellaneous botanical notes and characters. Proc. Amer. Acad. 8: 282–296.

______. 1872. Botanical contributions. Proc. Amer. Acad. 8: 365–412.

______. 1873. Characters of new genera and species of plants. Proc. Amer. Acad. 8: 620–661.

______. 1874. Notes on Compositae and characters of certain genera and species. Proc. Amer. Acad. 9: 187–218.

______. 1874. Contributions to the botany of North America. Proc. Amer. Acad. 10: 39–78.

______. 1875. A conspectus of the North American Hydrophyllaceae. Proc. Amer. Acad. 10: 312–332.

______. 1876. Miscellaneous botanical contributions. Proc. Amer. Acad. 11: 71–104.

______. 1876. Contributions to the botany of North America—V. Proc. Amer. Acad. 12: 51–84.

______. 1876. Geological survey of California. Botany. Vol. 1. ed. 1.

______. 1878. Synoptical flora of North America. Vol. II - Part 1. New York: Ivison, Blakeman, Taylor and Co. 402 pp.

______. 1878. Contributions to the botany of North America. Proc. Amer. Acad. 13: 361–374.

______. 1880. Geological survey of California. Botany. Vol. 1. 628 pp.

______. 1880. Contributions to North American botany. Proc. Amer. Acad. 16: 78–108.

______. 1883. Contributions to North American botany. Proc. Amer. Acad. 19: 1–96.

______. 1884. Synoptical flora of North America. Vol. 1. Part 2. New York: Ivison, Blakeman, Taylor, and Co. 473 pp.

______. 1885. A revision of some Boragineous genera. Proc. Amer. Acad. 20: 257–286.

______. 1886. Contributions to American botany. Proc. Amer. Acad. 13: 363–413.

______. 1886. Synoptical flora of North America. Vol. 1. Ed. 2. Washington: Smithsonian Institution. 480 pp.

______. 1889. John Torrey. p. 359–369 *in* C. S. Sargent, Scientific papers of Asa Gray. Vol. 2. Essays; Biographical sketches. 1841–1886. Macmillan and Co.; London. 503 pp.

Greene, E. L. 1896. New or noteworthy species—XVII. Pittonia 3: 91–116.

______. 1896. Studies in the Cruciferae—I. Pittonia 3: 117–138.

______. 1897. Some Rocky Mountain asters. Pittonia 3: 212–224.

______. 1899. New or noteworthy species—XXIV. Pittonia 4: 68–72.

______. 1899. West American Asperifoliae—IV. Pittonia 4: 86–97.

______. 1900. A fascicle of Senecios. Pittonia 4: 108–124.

______. 1900. A fascicle of new *Arnicas*. Pittonia 4: 159–174.

______. 1901. New or noteworthy species—XXVIII. Pittonia 4: 233–241.

______. 1903. *Platystemon* and its allies. Pittonia 5: 139–194.

______. 1905. A proposed new genus, *Annotites*. Leafl. Bot. Obs. & Crit. 1: 97–112.

______. 1905. Segregates of the genus *Rhus*. Leafl. Bot. Obs. & Crit. 1: 114–144.

______. 1905. New species of *Penstemon*. Leafl. Bot. Obs. & Crit. 1: 161–176.

______. 1905. Revision of *Eschscholtzia*. Pittonia 5: 205–293.

______. 1905. Diagnoses Aragallorum. Proc. Biol. Soc. Washington 18: 11–18.

______. 1906. The genus *Ptelea* in the western and southwestern United States and Mexico. Contr. U.S. Natl. Herb. 10: 49–78.

______. 1906. A study of *Rhus glabra*. Proc. Washington Acad. 8: 167–196.

______. 1908. Novitates borealis Americanae—II. Feddes Repert. 5: 241–244.

______. 1909. New western Asteraceae. Leafl. Bot. Obs. & Crit. 2: 8–13.

______. 1910. Some western caulescent violets. Leafl. Bot. Obs. & Crit. 2: 32–34.

______. 1910. Miscellaneous specific types—I. Leafl. Bot. Obs. & Crit. 2: 45–48.

______. 1910. Some western species of *Arabis*. Leafl. Bot. Obs. & Crit. 2: 69–88.

______. 1910. Studies of Thalictraceae—II. Leafl. Bot. Obs. & Crit. 2: 89–94.

______. 1912. New species of *Chaenactis*. Leeafl. Bot. Obs. & Crit. 2: 221–225.

______. 1912. Novitates borealii Americanae—VI. Species novae generis *Cercidis*. Feddes Repert. 11: 108–111.

Greenman, J. M. 1914. Descriptions of North American Senecioneae. Ann. Missouri Bot. Gard. 1: 263–290.

______. 1916. Monograph of the North and Central American species of the genus *Senecio*. Part II. Ann. Missouri Bot. Gard. 3: 85–194.

______. 1917. Monograph of the North and Central American species of the genus *Senecio*. Part II. Ann. Missouri Bot. Gard. 4: 15–36.

Greenman, J. M., and E. M. F. Roush. 1929. New *Agaves* from southwestern United States. Ann. Missouri Bot. Gard. 16: 389–392.

Hackel, E. 1896. *Festuca dasyclada*. Page 602 *in* W. J. Beal, Grasses of North America Vol. 2. New York, Henry Holt and Company.

Hall, H. M., and F. E. Clements. 1923. The phylogenetic method in Taxonomy. The North American species of *Artemisia*, *Chrysothamnus*, and *Atriplex*. Carnegie Institution of Washington. 355 pp.

Hanks, L. T. and J. K. Small. 1907. Geraniaceae. N. Amer. Fl. 25: 3–24.

Hanson, C. A. 1962. New species of perennial *Atriplex* from the western United States. Stud. Syst. Bot. (BRY) 1: 1–4.

Heil, K. 1979. Three new species of Cactaceae from southeastern Utah. Cact. & Succ. J. (U.S.) 51: 25–30.

Heimerl, A. 1902. *Abronia fallax*. Page 684 *in* P. A. Rydberg, Studies on the Rocky Mountain Flora—IX. Bull. Torrey Bot. Club 29: 680–693.

Heiser, C. B. 1961. A new annual sunflower, *Helianthus deserticolus*, from the southwestern United States. Proc. Indiana Acad. Sci. 70: 209–212.

Heller, A. A. 1905. Western species, new and old—IV. Muhlenbergia 1: 111–118.

Hermann, F. J. 1934. A new *Cardamine* from the Uinta Mountains, Utah. Rhodora 36: 409–412.

______. 1937. Extensions of range and a new species in *Carex*. Rhodora 39: 492–495.

Higgins, L. C. 1968. New species of perennial *Cryptantha* from Utah. Great Basin Naturalist 28: 195–198.

Hitchcock, A. S. 1933. New species and new names of grasses from Texas. J. Washington Acad. Sci. 23: 449–456.

Hitchcock, C. L. 1941. A revision of the *Drabas* of western North America. Univ. Washington Publ. Biol. 11: 1–120.

______. 1950. On the subspecies of *Lepidium montanum*. Madrono 10: 155–158.

______. 1952. A revision of the North American species of *Lathyrus*. Univ. Washington Publ. Biol. 15: 1–104.

Hitchcock, C. L., and B. Maguire. 1947. A revision of the North American species of *Silene*. Univ. Washington Publ. Biol. 13: 1–73.

Holm, T. H. 1891. A study of some anatomical characters of North American Gramineae - III. Bot. Gaz. 16: 275–281.

Holmgren, A. H., L. M. Shultz, and T. K. Lowrey. 1976. *Sphaeromeria*, a genus closer to *Artemisia* than to *Tanacetum* (Asteraceae: Anthemideae). Brittonia 28: 255–262.

Holmgren, N. H. 1973. Five new species of *Castilleja* (Scrophulariaceae) from the Intermountain Region. Bull. Torrey Bot. Club 100: 83–93.

______. 1978. Three new species of *Penstemon* (Scrophulariaceae) from the Intermountain region. Brittonia 30: 416–425.

______. 1979. New *Penstemons* (Scrophulariaceae) from the Intermountain region. Brittonia 31: 217–242.

Holmgren, N. H., and A. H. Holmgren. 1974. Three new species from the Great Basin. Brittonia 26: 309–315.

Holmgren N. H., and P. K. Holmgren. 1979. A new species of *Asclepias* (Asclepiadaceae) from Utah. Brittonia 31: 110–114.

Hopkins, M. 1937. *Arabis* in eastern and central North America. Rhodora 39: 106–148.

House, H. D. 1906. New and noteworthy North American species of *Trifolium*. Bot. Gaz. 41: 334–347.

Howell, J. T. 1940. New western Plants. Leafl. W. Bot. 2: 253.

______. 1943. Studies in *Phacelia*—a revision of species related to *P. pulchella* and *P. rotundifolia*. Amer. Midl. Naturalist 29: 1–26.

Ives, J. C. 1860. Report upon the Colorado River of the west. Washington D.C. C. Wendell, Printers.

Johnston, I. M. 1923. Diagnoses and notes relating to the spermatophytes chiefly of North America. Contr. Gray Herb. II, 68: 80–104.

______. 1937. Studies in the Boraginaceae—XII. J. Arnold Arb. 18: 1–25.

______. 1939. Studies in the Boraginaceae—XIII. J. Arnold Arb. 20: 375–402.

______. 1948. Studies in the Boraginaceae—XVI. Species chiefly from Mexico and western United States. J. Arnold Arb. 29: 227–241.

______. 1952. Studies in the Boraginaceae—XXII. Noteworthy species, chiefly Asian and South American. J. Arnold Arb. 33: 62–78.

Jones, A. J., and M. J. Broaddus. 1952?. V. Marcus Eugene Jones, 1852–1934 (Mark). *In* A. J. Jones, Publius Virgilius and Lavinia (Burton) Jones and their family—1800–1950. Published by the family; without locality designated.

Jones, M. E. 1881. Notes from Utah. Bull. Torrey Bot. Club 8: 70–71.

______. 1891. New plants from Arizona, Utah and Nevada. Zoe 2: 12–17.

______. 1891. New species and notes of Utah plants. Zoe 2: 236–252.

______. 1893. Contributions to western botany, No. 3. Zoe 3: 283–309.

______. 1893. Contributions to western botany, No. 4. Zoe 4: 22–54.

______. 1893. Contributions to western botany, No. 5. Zoe 4: 254–282.

______. 1894. Contributions to western botany, No. 6. Zoe 4: 366–369.

______. 1895. Contributions to western botany, No. 7. Proc. Calif. Acad. II, 5: 611–733.

______. 1898. Contributions to western botany, No. 8. Contr. W. Bot. 8: 1–43.

______. 1902. Contributions to western botany, No. 10. Contr. W. Bot. 10: 1–90.

______. 1903. Contributions to western botany, No. 11. Contr. W. Bot. 11: 1–22.

______. 1908. Contributions to western botany, No. 12. Contr. W. Bot. 12: 1–97.

______. 1910. New species and notes. Contr. W. Bot. 13: 1–87.

______. 1912. Contributions to western botany, No. 14. Contr. W. Bot. 14: 1–52.

______. 1923. Revision of North American species of *Astragalus*. Salt Lake City; by the author. 288 pp.

______. 1929. Contributions to western botany. No. 15. Contr. W. Bot. 15: 1–163.

______. 1930. Contributions to western botany. No. 16. Contr. W. Bot. 16: 1–53.

______. 1933. Contributions to western botany. No. 18. New species and notes. Contr. W. Bot. 18: 20–130.

Kearney, T. H. 1898. Studies on American grasses. Revision of North American species of *Calamogrostis*. U.S.D.A Agrostol. Bull. 11: 1–62.

Keck, D. D. 1934. A new *Penstemon* from Utah. Leafl. W. Bot. 1: 82–83.

______. 1937. Studies in *Penstemon*—IV. The section Ericopsis. Bull. Torrey Bot. Club 64: 357–381.

______. 1937. Studies in *Penstemon*—V. The section Peltanthera. Amer. Midl. Naturalist 18: 790–829.

______. 1940. Studies in *Penstemon*—VII. The subsections Gairdneriani, Deusti, and Arenarii of the Graciles, and miscellaneous new species. Amer. Midl. Naturalist 23: 594–616.

Klein, W. 1962. New taxa and recombinations in *Oenothera* (Anogra). Aliso 5: 179–180.

Koehne, B. A. E. 1890. *Amelanchier utahensis*. Wiss. Bei. Progr. Falk-Realgym. Berl. 95: 25.

Kuntze, C. E. O. 1885. Monographie der Gattung *Clematis*. Verh. Bot. Ver. Brandenb. 26: 84–202.

______. 1891–95. Revisio generum plantarum. Vol. I & II. Leipzig. 1011 pp.

Leveille, H. 1908. Monographie du genre *Oenethera*. Bull. Acad. Internat. Geogr. Bot. 17: 257–332.

Macbride, J. F. 1916. *Mertensias* of western North America. Contr. Gray Herb. II, 48: 1–20.

______. 1916. Revision of the genus *Oreocarya*. Contr. Gray Herb. II, 48: 20–38.

Macbride, J. F., and E. B. Payson. 1917. A revision of the *Erigerons* of the series *multifida*. Contr. Gray Herb. II, 49:72–79.

MacKenzie, K. K. 1917. *Carex epapillosa*. Page 138 *in* P. A. Rydberg, Flora of the Rocky Mountains. New York: by the author.

Maguire, B. 1941. Great Basin plants—III. Caryophyllaceae. Madrono 6: 22–27.

______. 1942. Great Basin plants—VII. Cruciferae. Amer. Midl. Naturalist 27: 463–469.

______. 1944. Great Basin plants—VIII. New species in *Carex* and *Erigeron*. Brittonia 5: 199–202.

______. 1946. Studies in the Caryophyllaceae—I. Bull. Torrey Bot. Club 73: 326.

______. 1947. Great Basin plants—IX. Compositae. *Arnica*, *Hymenopappus*, *Haplopappus*, and *Lygodesmia*. Amer. Midl. Naturalist 37: 136–145.

______. 1947. Studies in the Caryophyllaceae—III. A synopsis of the North American species of *Arenaria*. Bull. Torrey Bot. Club 74: 38-56.

______. 1951. Studies in the Caryophyllaceae—IV. *Arenaria* in America north of Mexico, a conspectus. Amer. Midl. Naturalist 46: 493–511.

Maguire, B. and A. Cronquist. 1947. *Erigeron flagellaris* var. *trilobatus*. Page 258 *in* A. Cronquist, Revision of the North American species of *Erigeron*, north of Mexico. Brittonia 6: 121–302.

Maguire, B. and G. H. Jensen. 1942. Great Basin plants—V. Aquatics. Rhodora 44: 5–10.

Maguire, B. and A. H. Holmgren. 1946. Botany of the Intermountain Region—I. Leafl. W. Bot. 4: 261–267.

Maguire, B. and R. E. Woodson. 1941. Two new Asclepiads from the southwestern United States. Ann. Missouri Bot. Gard. 28: 245.

Marshall, W. T. 1954. *Pediocactus hermannii* sp. nov. Saguaroland Bull. 8: 78–81.

Martin, R. F. 1940. A new *Juncus* from Utah. Rhodora 40: 69–70.

Mathias, M. E. 1930. Studies in Umbelliferae III. A monograph of *Cymopterus* including a critical study of related genera. Ann. Missouri Bot. Gard. 17: 213–474.

______. 1932. Studies in the Umbelliferae. IV. A new species of *Cogswellia*. Ann. Missouri Bot. Gard. 19: 497–498.

McKelvey, S. D. 1947. Yuccas of the southwestern United States. Part 2. Jamaica Plain; Arnold Arboretum. 192 pp.

McVaugh, R. 1956. Edward Palmer. Plant Explorer of the American West. Norman: University of Oklahoma Press. 430 pp.

Mez, C. C. 1921. *Stipa mormonum.* Feddes Repert. 17: 209.

Morton, C. V. 1937. *Physaria grahamii.* Page 26 *in* E. H. Graham, Botanical studies in the Uinta Basin of Utah and Colorado. Ann. Carnegie Mus. Vol. 26.

Munz, P. A. 1928. Studies in Onagraceae—I. A revision of the subgenus Chylismia of the genus *Oenothera.* Amer. J. Bot. 15: 223-240.

______. 1931. Studies in Onagraceae—VII. The subgenus Pachylophus of the genus *Oenothera.* Amer. J. Bot. 18: 728-738.

______. 1965. Botanical exploration of Marcus E. Jones. Leafl. W. Bot. 10: 193-236.

Murray, E. 1980. *Acer* notes No. 9. Kalmia 10: 2.

Neese, E. J., and S. L. Welsh. 1981. *Astragalus* section Desperati and a new species from the Uinta Basin of Utah. Rhodora 83: 455-460.

Nelson, A. 1899. New plants from Wyoming—VII. Bull. Torrey Bot. Club 26: 236-250.

______. 1900. Some Rocky Mountain Chrysothamni. Bot. Gaz. 28: 369-377.

______. 1900. Contributions from the Rocky Mountain herbarium—I. Bot. Gaz. 30: 189-203.

______. 1902. Contributions from the Rocky Mountain herbarium—IV. Chenopodiaceae. Bot. Gaz. 34: 355-371.

______. 1904. Contributions from the Rocky Mountain herbarium—V. Bot. Gaz. 37: 260-279.

______. 1904. New plants from Nevada. Proc. Biol. Soc. Washington 17: 91-98.

______. 1906. Contributions from the Rocky Mountain herbarium VII. Bot. Gaz. 42: 48-54.

______. 1907. Some new western plants and their collectors. Proc. Biol. Soc. Washington 20: 33-40.

______. 1912. Contributions from the Rocky Mountain herbarium—XI. New plants from Idaho. Bot. Gaz. 54: 138-151.

______. 1913. Contributions from the Rocky Mountain herbarium—XIII. Bot. Gaz. 56: 61-71.

______. 1922. Flora of the Navajo Indian Reservation—II. Amer. Botanist 28: 20-25.

______. 1924. Taxonomic studies—miscellaneous new species. Univ. Wyoming Publ. Bot. 1: 63-68.

______. 1926. Miscellaneous new species. Univ. Wyoming Publ. Sci. Bot. 1: 122-143.

______. 1934. Rocky Mountain herbarium studies—II. Amer. J. Bot. 21: 573-582.

______. 1936. Rocky Mountain herbarium studies—IV. Amer. J. Bot. 23: 265-271.

______. 1945. Rocky Mountain herbarium studies—VI. Amer. J. Bot. 32: 284-290.

Nelson, A., and J. F. Macbride. 1916. Western plant studies—III. Bot. Gaz. 61: 30-47.

Nelson, E. 1899. Revision of the North American *Phloxes.* Laramie; by the author. 35 pp.

______. 1901. A revision of certain species of plants of the genus *Antennaria.* Proc. U.S. Natl. Museum 23: 697-713.

Norton, J. B. S. 1899. North American species of *Euphorbia*, section Tithymalus. Eleventh Annual Report. Missouri Bot. Gard. 144 pp.

Osterhout, G. E. 1926. *Oreocarya breviflora.* Page 169 *in* E. B. Payson, *Thlaspi, Oreocarya,* and *Erigeron.* Univ. Wyoming Publ. Bot. 1: 145-186.

Ottley, A. M. 1944. The American Loti with special consideration of a proposed new section, Simpeteria. Brittonia 5: 81-123.

Ownbey, G. B. 1958. Monograph of the genus *Argemone* for North America and the West Indies. Mem. Torrey Bot. Club 21(1):1-159.

Parry, C. C. 1875. Botanical observations in southern Utah in 1874. Amer. Naturalist 9: 14-21, 139-146, 199-205, 267-273, 346-351.

______. 1878. Botanical Collection. Proc. Davenport Acad. Nat. Sci. 2: 279-282.

Payson, E. B. 1915. New and noteworthy plants from southwestern Colorado. Bot. Gaz. 60: 374-382.

______. 1921. A monograph of the genus *Lesquerella.* Ann. Missouri Bot. Gard. 8: 103-236.

______. 1926. *Thlaspi, Oreocarya,* and *Erigeron.* Univ. Wyoming Publ. Bot. 1: 145-186.

Pennell, F. W. 1920. Scrophulariaceae of the central Rocky Mountain states. Contr. U.S. Natl. Herb. 20: 313-381.

______. 1933. A revision of *Synthyris* and *Besseya.* Acad. Nat. Sci. Philadelphia 85: 77-106.

______. 1935. The Scrophulariaceae of eastern temperate North America. Acad. Nat. Sci. Philadelphia Monogr. 1: 1-650.

Petrak, F. 1917. Die nordamerikanischen Arten der Gattung *Cirsium.* Beih. Bot. Centralbl. 35(2): 223-567

Pilger, R. K. F. 1922. Uber die Formen von *Plantago major* L. Feddes Repert. 18: 277.

Piper, C. V. 1899. New and noteworthy Northwestern plants—II. Erythea 7: 159-163.

Porter, C. L. 1952. Novelties in *Hermidium* (Nyctaginaceae) and *Astragalus* (Leguminosae) from eastern Utah. Rhodora 54: 158-161.

Preston, C. H. 1897. Biographical sketch of Dr. C. C. Parry. Proc. Davenport Acad. Nat. Sci. 6: 35-45.

Purpus, J. A. 1900. Die Succulenten der La Sal Mountains in Utah. Monats. Kakteenk. 10: 95-97.

______. 1900. Die Succulenten der La Sal Mountains in Utah. Monats. Kakteenk. 10: 110-112.

______. 1909. *Opuntia utahensis* J. A. Purpus nov. spec. Monats. Kakteenk. 19: 133-135.

Raven, P. H. 1962. The systematics of *Oenothera* subgenus Chylismia. Univ. Calif. Publ. Bot. 34: 1-122.

______. 1969. A revision of the genus *Camissonia* (Onagraceae). Contr. U.S. Natl. Herb. 37: 161-396.

Rechinger, K. H. 1936. *Rumex utahensis.* Feddes Repert. 40: 298.

Reveal, J. L. 1965. Notes on three Utah *Eriogonums.* Proc. Utah Acad. 42: 287-292.

______. 1967. Notes on *Eriogonum*—V. A revision of the *Eriogonum corymbosum* complex. Great Basin Naturalist 27: 183-229.

______. 1968. A new annual *Eriogonum* from Utah. Ann. Missouri Bot. Gard. 55: 74-75.

______. 1969. New species of *Eriogonum* from Utah. Madrono 19: 289-300.

______. 1972. Descriptions of new species and combinations in *Eriogonum* (Polygonaceae). Phytologia 23: 163–178.

______. 1973. *Eriogonum* (Polygonaceae) of Utah. Phytologia 25: 169–217.

______. 1974. Two shrubby novelties in *Eriogonum* (Polygonaceae) from the deserts of Utah and Arizona. Brittonia 26: 90–94.

______. 1974. Two new varieties of *Eriogonum* (Polygonaceae) from the Intermountain Region. Great Basin Naturalist 34: 245–246.

______. 1976. *Eriogonum* (Polygonaceae) of Arizona and New Mexico. Phytologia 35: 409–483.

______. 1977. *Yucca angustissima* var. *avia*. Intermountain Flora 6: 534.

______. 1981. A new pulvinate *Eriogonum* (Polygonaceae) from Utah. Great Basin Naturalist 41: 229–231.

Robbins, J. W. 1871. *Potamogeton*. Pages 247–340 *in* S. Watson, Botany. Report of U.S. Geological Exploration of the Fortieth Parallel. 5: xiii–525.

Robinson, B. L. 1917. A monograph of the genus *Brickelia*. Mem. Gray Herb. 1: 1–151.

Robinson, B. L., and J. M. Greenman. 1899. Revision of the genus *Gymnolomia*. Proc. Boston Soc. Nat. Hist. 29: 87–100.

Rollins, R. C. 1939. The Cruciferous genus *Physaria*. Rhodora 41: 392–414.

______. 1940. Studies in the genus *Hedysarum* in North America. Rhodora 42: 217–239.

______. 1941. Some new or noteworthy North American crucifers. Contr. Dudley Herb. 3: 174–183.

______. 1941. Monographic study of *Arabis* in western North America. Rhodora 43: 289–485.

______. 1955. The auriculate-leaved species of *Lesquerella* (Cruciferae). Rhodora 57: 241–264.

______. 1971. Protogyny in the Cruciferae and notes on *Arabis* and *Caulanthus*. Contr. Gray Herb. 201: 3–10.

______. 1981. Studies on *Arabis* (Cruciferae) of western North America. Systematic Botany 6: 55–64.

Rosendal, C. O., F. K. Butters, and O. Lakela. 1936. *Heuchera versicolor* f. *pumila*. Minnesota Studies Plant Sci. 2: 85.

Rydberg, P. A. 1897. Notes on Potentilla—VI. Bull. Torrey Bot. Club 24: 1–13.

______. 1900. Catalogue of the flora of Montana and the Yellowstone National Park. Mem. New York Bot. Gard. 1: i–492.

______. 1900. Studies on the Rocky Mountain Flora—I. Bull. Torrey Bot Club 27: 169–189.

______. 1900. Studies on the Rocky Mountain Flora—II. Bull. Torrey Bot. Club 27: 614–636.

______. 1900. Studies on the Rocky Mountain Flora—III. Some smaller genera of composites. Bull. Torrey Bot. Club 27: 614–636.

______. 1901. The oaks of the continental divide north of Mexico. Bull. New York Bot. Gard. 2: 187–233.

______. 1902. Studies on the Rocky Mountain Flora—VII. Bull. Torrey Bot. Club 29: 145–160.

______. 1902. Studies on the Rocky Mountain Flora—VIII. Bull. Torrey Bot. Club 29: 232–246.

______. 1902. Studies on the Rocky Mountain Flora—IX. Bull. Torrey Bot. Club 29: 680–693.

______. 1903. Studies on the Rocky Mountain Flora—X. Bull. Torrey Bot. Club 30: 247–262.

______. 1903. Some generic segregations. Bull. Torrey Bot. Club 30: 271–281.

______. 1904. Studies on the Rocky Mountain Flora—XII. Bull. Torrey Bot. Club 31: 555–575.

______. 1904. Studies on the Rocky Mountain Flora—XIII. Bull. Torrey Bot. Club 31: 631–655.

______. 1905. Studies on the Rocky Mountain Flora—XIV. Bull. Torrey Bot. Club 32: 123–138.

______. 1905. *Astragalus* and its segregates as represented in Colorado. Bull. Torrey Bot. Club 32: 657–668.

______. 1907. Studies on the Rocky Mountain Flora—XVII. Bull. Torrey Club 34: 35–50.

______. 1907. Studies on the Rocky Mountain Flora—XVIII. Bull. Torrey Bot. Club 34: 417–437.

______. 1908. Rosaceae—III & IV. N. Amer. Fl. 22: 239–387.

______. 1909. Studies on the Rocky Mountain Flora—XX. Bull. Torrey Bot. Club 36: 675–698.

______. 1910. Studies on the Rocky Mountain Flora—XXI. Bull. Torrey Bot. Club 37: 127–148.

______. 1910. Studies on the Rocky Mountain Flora—XXII. Bull. Torrey Bot. Club 37: 313–335.

______. 1910. Studies on the Rocky Mountain Flora—XXIII. Bull. Torrey Bot. Club 37: 443–471.

______. 1910. Studies on the Rocky Mountain Flora—XXIV. Bull. Torrey Bot. Club 37: 541–557.

______. 1911. Studies on the Rocky Mountain Flora—XXV. Bull. Torrey Bot. Club 38: 11–23.

______. 1912. Studies on the Rocky Mountain Flora—XXVI. Bull. Torrey Bot. Club 39: 99–111.

______. 1912. Studies on the Rocky Mountain Flora—XXVII. Bull. Torrey Bot. Club 39: 301–328.

______. 1913. Studies on the Rocky Mountain Flora—XXVIII. Bull. Torrey Bot. Club 40: 43–74.

______. 1913. Studies on the Rocky Mountain Flora—XXIX. Bull. Torrey Bot. Club 40: 461–485.

______. 1913. Rosaceae—V. N. Amer. Fl. 22: 389–479

______. 1914. (Carduales) Carduaceae. Helenieae. N. Amer. Fl. 34: 1–80.

______. 1915. *Gaillardia*. N. Amer. Fl. 34: 131–140.

______. 1917. Notes on Rosaceae—XI. Roses of California and Nevada. 44: 65–84.

______. 1917. Flora of the Rocky Mountains. New York; by the author. 1143 pp.

______. 1922. Flora of the Rocky Mountains. ed. 2. New York: by the author. 1143 pp.

______. 1925. Notes on Fabaceae—V. Bull. Torrey Bot. Club 52: 229–235.

______. 1927. Senecioneae. N. Amer. Fl. 34: 309–360.

______. 1929. (Rosales) Fabaceae, Galageae. N. Amer. Fl. 24: 315–462.

______. 1929. Scylla or Charybdis. Proc. International Congress Plant Sciences. 2: 1539–1551.

St.-Yves, A. 1925. Contribution a L' etude des *Festuca* (Subgenus Eu-Festuca) de l' Amerique du Nord et du Mexico. Candollea 2: 229–316.

Schneider, C. K. 1905. Beitrag zur Kenntnis der Arten und Formen der Gattung *Cercocarpus* Kunth. Mitt. Deutsch. Dendrol. Gesells. 14: 125–129.

______. 1905. Illustriertes Handbuch der Laubholzkunde. Vol. I. Jena. Part 2: 449–592.

Schulz, O. E. 1903. Monographie der gattung *Cardamine*. Bot. Jahrb. Syst. 32: 417–623.

______. 1924. *Descurainia*. Pflanzenr. 4, Fam. 105 (Heft 86): 304–346.

———. 1927. Draba—Section XII. Phyllodraba. Pflanzenr. 4, Fam. 105 (Heft 89): 173–198.

Scribner, F. L. 1911. Notes on certain species of *Muhlenbergia*. Bull. Torrey Bot. Club 38: 319–328.

Scribner, F. L. and T. A. Williams. 1899. New species of North American Grasses. U.S.D.A. Agrostol. Circ. 9. 7 pp.

Sharp, 1935. A critical study of certain epappose genera of the Heliantheae-Verbesininae of the natural family Compositae. Ann. Missouri Bot. Gard. 22: 51–152.

Sheldon, E. P. 1894. A preliminary list of the North American species of *Astragalus*. Bull. Geol. & Nat. Hist. Surv. Minn. 9: 116–175.

Shultz, L. M. and J. Shultz. 1981. A new species of *Hackelia* (Boraginaceae) from Utah. Brittonia 33: 159–161.

Slosson, M. 1914. Notes on two North American ferns. Bull. Torrey Bot. Club 41: 307–309.

Small, J. K. 1896. *Oenothera* and its segregates. Bull. Torrey Bot. Club 23: 167–194.

———. 1898. Studies in North American Polygonaceae. Bull. Torrey Bot. Club 25: 40–53.

———. 1905. Hydrangeaceae. N. Amer. Fl. 22: 159–178.

Small, J. K. and P. A. Rydberg. 1905. Saxifragaceae. N. Amer. Fl. 22: 81–158.

Smiley, F. J. 1916. *Mertensia praecox*. Page 10 *in* J. F. Macbride, *Mertensias* of western North America. Contr. Gray Herb. II, 48: 1–20.

Smith, C. P. 1912. Notes from northern Utah—IV. Muhlenbergia 7: 136–138.

———. 1948. Lupinus. Sp. Lupinorum 36: 625–640.

———. 1949. Lupinus. Sp. Lupinorum 38: 657–672.

———. 1951. Lupinus. Sp. Lupinorum 40: 689–704.

Smith, J. G. 1899. Studies on American grasses: synopsis of genus *Sitanion*. U.S.D.A. Agrostol. Bull. 18: 1–21.

Standley, P. C. 1916. Chenopodiales, Chenopodiaceae. N. Amer. Fl. 21: 1–93.

Stansbury, H. 1852. Exploration and survey of the valley of the Great Salt Lake of Utah. Philadelphia. Lippincott, Grambo and Co.

St. John, H. 1915. *Rumex persicarioides* and its allies in North America. Rhodora 17: 73–83.

Stockwell, P. 1940. A revision of the genus *Chaenactis*. Contr. Dudley Herbarium 3: 89–168.

Stokes, S. G. 1936. The genus *Eriogonum*, a preliminary study based on geographical distribution. San Francisco. J. H. Neblett Press.

Suksdorf, W. N. 1931. Untersuchungen in der gattung *Amsinkia*. Werdenda 1: 47–113.

Swallen, J. R. 1931. *Crassipes*, a new grass genus from Utah. Amer. J. Bot. 18: 684–685.

Thurber, G. 1871. *Vilfa depauperata* var. *filiformis*. Page 376 *in*: S. Watson, Botany. Report of U.S. Geological Survey of the Fortieth Parallel. 5: xiii–525.

Tidestrom, I. 1910. Species of *Aquilegia* growing in Utah and in adjacent portions of Colorado, Idaho and Arizona. Amer. Midl. Naturalist 1: 165–196.

———. 1913. A new *Salicornia*. Proc. Biol. Soc. Washington 26: 13.

———. 1913. Novitates florae utahensis. Proc. Biol. Soc. Washington 26: 121–122.

———. 1914. A new *Delphinium* from Utah. Proc. Biol. Soc. Washington 27: 61.

———. 1923. New or noteworthy species of plants from Utah and Nevada. Proc. Biol. Soc. Washington 36: 181–184.

Torrey, J. 1852. Catalogue of plants collected in the expedition. Pages 381–397 *in* H. Stansbury, Exploration and survey of the valley of the Great Salt Lake of Utah. Philadelphia. Lippincott, Grambo and Co.

———. 1871. Species of *Fraxinus*, and *Phacelia*. Pages 251,253,283. *in* S. Watson. Botany. Report of U.S. Geological Survey of the Fortieth Parallel. 5: xiii–525.

Torrey, J., and J. C. Fremont. 1845. Pages 311–320 *in* J. C. Fremont, Descriptions of some new genera and species of plants, collected in Capt. J. C. Fremont's exploring expedition to Oregon and north California in the years 1843–44. House Rep. Doc. 199.

Torrey, J., and A. Gray. 1855. Report on the botany of the expedition. Pages 115–132 *in* E. G. Beckwith, Report of explorations for a route for the Pacific Railroad, on the line of the forty-first parallel of north latitude. Reports of explorations and surveys, to ascertain the most practicable and economical route for a railroad from the Mississippi Roiover to the Pacific Ocean. 334d Cong., 2nd Sess., House Rep. Ex. Doc. Vol. 11, no 91.

———. 1870. A revision of the Eriogonea. Proc. Amer. Acad. 8: 145–200.

Trelease, W. O. 1902. The Yucceae. Rep. Missouri Bot. Gard. 13: 27–133.

———. 1907. Additions to the genus *Yucca*. Ann. Missouri Bot. Gard. 18: 225–230.

Tuzson, J. 1921. *Arabis hirsuta* f. *laevis*. Bericht Freien Verein. Pflanzengeogr. Syst. Bot. 1919: 43. 1921.

Underwood, L. M. 1898. *Selaginella rupestris* and its allies. Bull. Torrey Bot. Club 25: 125–133.

Vasey, G. 1876. A catalogue of the forest trees of the United States which usually attain a height of sixteen feet or more. Washington. Govt. Printing Office.

———. 1893. Descriptions of new or noteworthy grasses from the United States. Contr. U.S. Natl. Herb. 1: 267–281.

Voss, J. W. 1937. A revision of the *Phacelia* crenulata group for North America. Bull. Torrey Bot. Club 64: 133–144.

Wagner, W. L. 1981. *Oenothera acutissima* (Onagraceae), a new species from northwestern Colorado and adjacent Utah. Systematic Botany 6: 153–158.

Ward, L. F. 1876. General notes. 1—botany. Amer. Naturalist 10: 552–555.

Watson, E. E. 1929. Contributions to a monograph of the genus *Helianthus*. Papers Michigan Acad. Sci. 9: 305–475.

Watson, S. 1871. Botany. *In* C. King. Report of the Geological Exploration of the Fortieth Parallel. 5: xiii–525. Washington: Government Printing Office.

———. 1871. Descriptions of new species of plants, with revisions of certain genera. Proc. Amer. Acad. 12: 246–278.

______. 1873. Revision of the extra-tropical North American species of the genus *Lupinus*. Proc. Amer. Acad. 8: 517–548.

______. 1873. Revision of the extra-tropical North American species of the genus *Potentilla*. Proc. Amer. Acad. 8: 549–573.

______. 1873. New plants of northern Arizona and the region adjacent. Amer. Naturalist 7: 299–303.

______. 1873. Revision of the extra-tropical North American species of the genus *Oenothera*. Proc. Amer. Acad. 8: 573–618.

______. 1874. A revision of the North American Chenopodiaceae. Proc. Amer. Acad. 9: 82–126.

______. 1874. Contributions to the botany of North America—characters of various new species. Proc. Amer. Acad. 10: 68–78.

______. 1875. Revision of the genus *oCeanothus*, and description of new plants. Proc. Amer. Acad. 10: 333–350.

______. 1876. Botanical contributions—VI. Proc. Amer. Acad. 11: 105–148.

______. 1876. Geological Survey of California. Botany. Vol. 1. ed. 1.

______. 1877. Descriptions of new species of plants, with revisions of certain genera. Proc. Amer. Acad. 21: 246–278.

______. 1878. Bibliographical index to North American botany. Washington, D.C. Smithsonian Institution. 476 pp.

______. 1879. Contributions to American botany. Proc. Amer. Acad. 14: 213–303.

______. 1888. Contributions to American botany. Proc. Amer. Acad. 23: 249–287.

WATSON, T. J., JR. 1977. The taxonomy of *Xylorhiza* (Asteraceae—Astereae). Brittonia 29: 199–216.

WEBER, W. A. 1946. A taxonomic and cytological study of the genus *Wyethia*, family Compositae, with notes on the related genus *Balsomorhiza*. Amer. Midl. Naturalist 35: 400–452.

WELSH, S. L. 1970. An undescribed species of *Astragalus* (Leguminosae) from Utah. Rhodora 72: 189–193.

______. 1970. New and unusual plants from Utah. Great Basin Naturalist 30: 16–22.

______. 1971. Description of a new species of *Dalea* (Leguminosae) from Utah. Great Basin Naturalist 31: 90–92.

______. 1974. Utah plant novelties in *Astragalus* and *Yucca*. Great Basin Naturalist 34: 305–310.

______. 1976. Utah plant novelties in *Cymopterus* and *Penstemon*. Great Basin Naturalist 35: 377–378.

______. 1978. Endangered and threatened plants of Utah: A reevaluation. Great Basin Naturalist 38: 1–18.

______. 1978. Utah flora: Fabaceae (Leguminosae). Great Basin Naturalist 38: 225–367.

______. 1980. Utah flora: Malvaceae. Great Basin Naturalist 40: 27–37.

______. 1981. New taxa of western plants—in tribute. Brittonia 33: 294–303.

______. 1982. Utah Flora: Rosaceae. Great Basin Naturalist (in preparation).

WELSH, S. L., AND N. D. ATWOOD. 1977. An undescribed species of *Thelypodiopsis* (Brassicaceae) from the Uinta Basin, Utah. Great Basin Naturalist 37: 95–96.

WELSH, S. L., AND R. C. BARNEBY. 1981. *Astragalus lentiginosus* (Fabaceae) revisited—a unique new variety. Isleya 2: 1–2. 1981.

WELSH, S. L., AND S. GOODRICH. 1980. Miscellaneous plant novelties from Alaska, Nevada, and Utah. Great Basin Naturalist 40: 78–88.

WELSH, S. L., AND G. MOORE. 1968. Plants of Natural Bridges National Monument. Proc. Utah Acad. 45: 220–248.

WELSH, S. L., AND J. L. REVEAL. 1968. A new species of *Townsendia* (Compositae) from Utah. Brittonia 20: 375–377.

______. 1977. Utah Flora: Brassicaceae (Cruciferae). Great Basin Naturalist 37: 279–365.

WELSH, S. L., N. D. ATWOOD, AND J. L. REVEAL. 1975. Endangered, threatened, extinct, endemic, and rare or restricted Utah vascular plants. Great Basin Naturalist 35: 327–374.

WHEELER, G. M. 1878. Report upon United States geographical surveys west of the one hundredth meridian. Vol. VI. Washington D.C. Government Printing Office. 404 pp.

WHERRY, E. T. 1943. *Microsteris*, *Phlox*, and an intermediate. Brittonia 5: 60–63.

______. 1944. New Phloxes from the Rocky Mountains and neighboring regions. Not. Nat. 146: 1–11.

WHITE, T. G. 1894. A preliminary revision of the genus *Lathyrus* in North and Central America. Bull. Torrey Bot. Club 21: 444–458.

WILLIAMS, L. O. 1932. Field and herbarium studies—I. Bull. Torrey Bot. Club 59: 427–429.

______. 1936. Revision of the western *Primulas*. Amer. Midl. Naturalist 17: 741–748.

WILLIAMS, T. A. 1899. *Poa fendleriana* and its allies. U.S.D.A. Agrostol. Circ. 10. 6 pp.

YUNCKER, T. G. 1960. Two new species of *Cuscuta* from North America. Brittonia 12: 38–40.

A NEW SPECIES OF *CRYPTANTHA* (BORAGINACEAE) FROM NEVADA

Kaye H. Thorne[1] and Larry C. Higgins[2]

Abstract.— Described as new is *Cryptantha welshii* Thorne & Higgins from the White River Valley of Nye County, Nevada.

During investigations of the flora of southern Nevada it became evident that a previously undescribed species of *Cryptantha* was present among the mound-forming inhabitants of the white tuffaceous deposits in the White River Valley in Nye County, Nevada. This silicious material is present as abandoned playa deposits along the margin of the White River Valley. The deposits support a very low density of plant cover, but the species are unique. Included among the inhabitants are *Frasera gypsicola*, *F. albomarginata*, *Lepidium nana*, *Artemisia pygmaea*, *Phlox tumulosa*, and *Leptodactylon caespitosum*. There are other low, caespitose plants among the assemblage, but they have broader distributions.

The species of *Cryptantha* is described as follows:

Cryptantha welshii Thorne & Higgins, sp. nov.

Species nova *Cryptantha hoffmannii* I. M. Johnston proxima a qua imprimis differt foliis pustulatis inferioribus nuculis brevioribus stylo superatis 1–2 mm plantis parvioribus et tenellis.

Caespitose perennial, 0.5–1.4 dm tall; stems several, erect, arising from a branched caudex, strigose to sericeus, underhair with spreading setae; leaves spatulate to oblanceolate, strigose or subtomentose, setose, those of the lower surface pustulate, gradually reduced upwards; inflorescence cylindrical, densely setose, strigose, uppermost cymes elongating at maturity; calyx segments lanceolate, densely setose, in anthesis 3–4 mm long, in fruit becoming 5–8 mm long; corolla white, fornices yellow, 0.5 mm long, the tube shorter than the calyx, 2.5–3 mm long, 4–5 mm wide; nutlets 4, or 1–3 by abortion, broadly pear shaped to somewhat lanceolate-ovate, 1.5–2.5 mm long, 1.5–2 mm wide, margins more or less in contact, dorsal surface muricate to tuberculate, with a broad rugose central ridge, ventral surface scarcely muricate, the scar shortly open, triangular, the margin not elevated; style 1–1.5 mm longer than the nutlets.

Type.— USA. Nevada: Nye County, White River Valley, 2.1 miles W of Sunnyside, on the road to Hot Creek Campground, T7N, R61E, S36, at 5150 ft (1567 m) elevation, exposed rounded ancient playa remnant of white "tuffaceous" material, occasionally mixed with sand and valley fill, 5 June 1979, K. H. Thorne and B. F. Harrison 578 (Holotype BRY; Isotypes WTU, NY).

Additional specimens: Nevada, Nye County, T7N, R62E, S31, White River Valley, Sunnyside Hot Creek Campground road, 2.5 miles W of Hwy 318, 5230 ft elev., salt desert shrub community, 30 June 1980, B. T. Welsh & K. H. Thorne 391 (BRY); Garden Valley, 18.4 mi S of Hot Creek Campground, in a *Chrysothamnus viscidiflorus–Artemisia* community, on whitish sandy clay slopes, 10 June 1980, B. F. Harrison & K. H. Thorne 13298 (BRY); White River Valley, 6.7 mi N of Hot Creek Campground, T7N, R61E, S17, on limestone hill in valley center, on white

---

[1] Herbarium, Life Science Museum, Brigham Young University, Provo, Utah 84602.

[2] Herbarium, Department of Biology, West Texas State University, Canyon, Texas 79015.

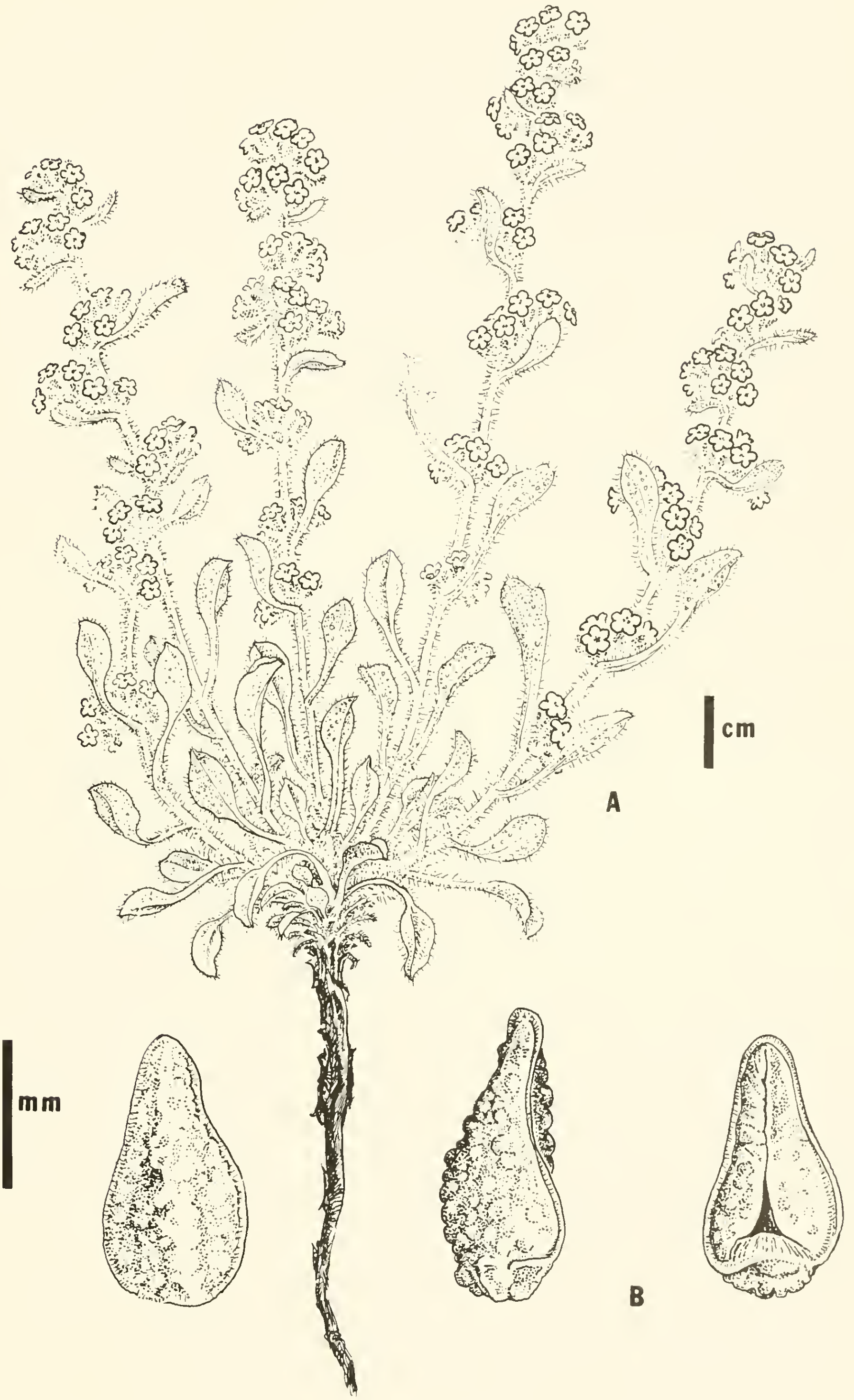


Fig. 1. *Cryptantha welshii* Thorne & Higgins: A, habitat of plant; B, seed (left to right) dorsal, side, and ventral views.

outcrops, 31 May 1980, K. H. Thorne & B. T. Welsh 897 (BRY). White Pine County, White River Valley, Jakes Wash, T15N, R60E, S24, pinyon-juniper and desert shrub communities with mound-forming plants on white tufaceous outcrops, 5 June 1980, K. H. Thorne et al. 987 (BRY).

Relationships of *Cryptantha welshii* apparently lie with *C. hoffmannii* Jtn. (Munz 1968). They are compared below:

1. Leaves pustulate on both surfaces; nutlets ovate 3–3.5 mm long, 2–2.5 mm wide; style exceeding nutlets 0.2–0.8 mm; plant robust .... *C. hoffmannii*

— Leaves pustulate on lower surface only; nutlets 1.5–2.5 mm long, 1.5–2 mm wide; style exceeding nutlets 1–2 mm; plant smaller, more delicate .... *C. welshii*

The known distributional area of *C. hoffmannii* is in the White Mountains and Westguard Pass areas of Inyo County, California (Higgins 1971).

The species is named in honor of Stanley L. Welsh, whose dedication to the study of the flora of the Intermountain and Great Basin regions has given a vast fund of new information concerning plant communities and rare or unusual plant species found in these regions. His help and encouragement are deeply appreciated.

LITERATURE CITED

HIGGINS, L. C. 1971. Revision of *Cryptantha* subgenus Oreocarya. BYU Sci. Bull. Biol. Ser. 13(4):1–63.

MUNZ, P. A. 1968. A California flora and supplement. Univ. of California Press, Berkeley, California.

NEW TAXA OF THISTLES (*CIRSIUM*; ASTERACEAE) IN UTAH

Stanley L. Welsh[1]

Abstract.— Described are several new taxa of the genus *Cirsium* that occur in the state of Utah: *C. eatonii* (Gray) Robins. var. *harrisonii* Welsh; *C. eatonii* var. *murdockii* Welsh; *C. ownbeyi* Welsh; *C. scariosum* Nutt. var. *thorneae*; and *C. virginensis* Welsh.

The thistles of Utah have long constituted one of the most difficult problems in the plant taxonomy of the state. Differences between taxa are often obscured by interspecific hybridization. Hybridization is not only between closely related entities, but occurs between species that have been placed in different sections of the genus. The problems of interpretation are compounded by the lack of a modern comprehensive treatment of our North American species. Previous treatments were based on few specimens and could not account for the variability as perceived by contemporary workers. Collectors have tended to avoid this genus and its relatives because of their spinescent and bulky nature. Only dedicated persons will trouble themselves with the specimens, which remain as problems even after they are deposited in herbaria. The pappus tends to expand, even in dry specimens, and the parachutelike apparatus floats about the herbarium every time someone moves the specimens from case to case or elsewhere.

Diagnostic criteria are, and have been, based on features that are inconstant. Features of the involucral bracts have been widely used to distinguish taxa in the group. Some of those features are better than others, including shape and dorsal surface texture. But others, including degree of development of the glandular dorsal crest and the presence of pubescence on the dorsal surface, have not proved reliable.

The following taxa have been distinguished while attempting to provide a treatment of the Utah thistles. The problems of our Utah materials often extend beyond the state, and I have had to examine materials from the surrounding states. The entire treatment will appear as a portion of the paper dealing with the Asteraceae (Compositae), which is in progress.

Cirsium eatonii **(Gray) Robins.** Eaton Thistle. [*Carduus eatonii* Gray]. Three more or less distinctive varieties are present.

1. Involucral bracts copiously gray- to brown-villous with long multicellular hairs; corollas ocroleucous; plants of the Uinta Mts. from Lake Fork eastward .. .. *C. eatonii* var. *murdockii*

— Involucral bracts merely white-tomentose or rarely with short multicellular hairs; corollas mainly pink or rose; plants of western Uinta Mts., and elsewhere 2

2(1). Involucral bracts commonly suffused with dark purple; involucres not obscured by outer spinose bracts; plants of the Tushar Mts. .... *C. eatonii* var. *harrisonii*

— Involucral bracts green or variously purplish; involucres with copious pinnate spines, mainly obscuring the surface of inner bractlets; plants of western Uinta and Wasatch mountains, and Great Basin ranges .... *C. eatonii* var. *eatonii*

---

[1] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Var. *harrisonii* Welsh var. nov. Similis *C. eatonii* var. *eatonii* sed bracteis atropurpureis suffusis et spinis paucioribus. TYPE.— USA. Utah: Piute Co., Tushar Mts., T28S, R4W, S8, alpine meadow, talus slope, igneous gravel, 3416 m elev., 16 Aug. 1978, Welsh & Henroid 18084 (Holotype BRY). Additional specimens: Utah. Piute Co., Tushar Mts., 9 mi due W Marysvale, T27S, R5W, S35, 3050 m elev, 27 July 1976, Welsh et al. 14030 (BRY); do, T27S, R5W, S1, 28 July 1967, Welsh et al. 14050 (BRY); do, 2989 m, 25 July 1978, Welsh et al. 17738 (BRY); do, T28S, R5W, S2, 17 Aug. 1978 (BRY). The few specimens of the Tushar Mountains phase seem to average smaller than in the type variety. They are isolated from the body of the species in the islandlike Tushar Mountains. The variety is named in honor of Professor Bertrand F. Harrison, teacher, collector, and authority on Utah grasses.

Var. *eatonii* [*C. eriocephalum* var. *leiocephalum* D. C. Eaton]. This is the basionym for *C. eatonii* in a strict sense, which was renamed by Gray in honor of D. C. Eaton, who collected with Sereno Watson in 1869. The lectotype came from the head of the Bear River, in Summit County (Watson 691, 1869 US!), with syntypical material being taken under the same number in Cottonwood Canyon (now Salt Lake County). Lodgepole pine and spruce communities upwards into alpine tundra at 2375 to 3420 m in Duchesne, Juab, Salt Lake, Summit, Tooele, and Weber counties; Nevada and Colorado. Specimens from the Deep Creek Mountains have few lateral spines on the outer bracts and approach *C. clavatum* in technical features. More material is needed to determine their status and relationships.

Var. *murdockii* Welsh var. nov. A *C. eatonii* var. *eatonii* differt in bracteis copiose griseis ad bruneis villosis pilis multicellulosis. TYPE.— USA. Utah: Duchesne Co.; Uinta Mts., Yellowstone Canyon, T4N, R5W, S25, 3355 m elev., Precambrian quartzite, 2 Aug. 1980, Welsh & Neese 19935 (Holotype BRY). Additional specimens: Utah. Duchesne Co.; Uinta Mts., Chepeta Lake vicinity, T5N, R1W, S28,29,32,33, spruce-lodgepole pine forest, 3233 m elev., 3 Aug 1980, Neese & Welsh 9455 (BRY); Chain Lake Basin, T4N, R4W, S23, 3377 m elev., 16 July 1979, Welsh et al. 19048 (BRY). Uintah Co., Uinta Mts., Leidy Peak, T1S, R19E, S6, 3660 m elev., Neese & Peterson 6395 (BRY); do, 30 July 1971, Waite 299 (BRY); do, White Rocks drainage, 17 July 1976, Goodrich 6478 (BRY). The plants grow in talus and rock stripes at 3230 to 3660 m in Daggett, Duchesne, and Uintah counties; endemic. The variety is named in honor of Professor Joseph Richard (Dick) Murdock, teacher and collector, whose ecological work on Oke Doke (Fifth Chain Lake) in the Uinta Mountains is classic. This variety has been regarded as constituting a portion of *C. tweedyi* (Rydb.) Petrak. That entity was reviewed by Moore and Frankton (1965) and was mapped to include northeastern Utah in its range. No specimens were cited from Utah, however. I have seen the type of that taxon, and other material within its range in northwest Wyoming, and they differ in pubescence of involucral bracts being merely white tomentose along the margins.

***Cirsium ownbeyi* Welsh sp. nov.** Ownbey Thistle. Perennial herbs from caudex and taproot, the caudex with marcescent dark brown leaf bases; leaves of basal rosettes 5–13 cm long, 1.5–3 cm wide, tripinnatifid, green on both sides, sparingly tomentose along lower side of midrib; cauline leaves with vesture and lobing like the basal; stems 5–7 dm tall, winged-decurrent, sparingly tomentose; involucres 1.8–2.5 cm high, 1.5–2.5 cm wide, the outermost bracts more or less pinnately spinose, lance-attenuate, smooth medially, the dorsal ridge not well developed, not scabrous, sparingly tomentose along margins, the inner more or less contorted apically; spines 3–8 mm long; corollas rose-pink.

Similis *Circio clavato* sed in caulibus alatis et foliis tripinnatifidis differt. TYPE.— USA. Utah: Uintah County, Horse Trail Canyon, T4S, R24E, S4, juniper-sagebrush community, 1678 m elev., 2 July 1955, Welsh 343 (Holotype BRY). Additional specimens: Utah. Daggett County, Crouse Canyon, T1N, R25E, S2, 15 June 1978, Neese 5673 (BRY). The Ownbey thistle is known from juniper, sagebrush, and riparian communities at 1678 to 1891 m in Daggett and Uintah counties. The species is named in honor of Dr. Gerald B. Ownbey, specialist in *Cirsium*, who first recognized the distinctive nature of this species. Relationships of the Ownbey thistle apparently lie with *C. eatonii.*

Cirsium scariosum **Nutt.** Meadow Thistle. [*Carduus lacerus* Rydb., type from near Midway; *Carduus olivescens* Rydb., type from the Aquarius Plateau; *Cirsium acaule* var. *americanum* Gray; *Cnicus drummondii* var. *acaulescens* Gray; *C. foliosum* authors, not T. & G.; *C. drummondii* authors, not T. & G.]. Our specimens fall into two rather distinctive varieties.

1. Heads 25–35 mm high, 35–80 mm wide; inner bracts slender, sometimes contorted, not especially dilated; plants mainly 6–12 dm tall .... *C. scariosum* var. *thorneae*

— Heads 22–30 mm high, 20–40 mm wide; inner bracts often dilated or contorted, sometimes fimbriate; plants 0–6 dm tall .... *C. scariosum* var. *scariosum*

Var. ***scariosum*** [*Cirsium acaule* var. *americanum* Gray]. This taxon, as here interpreted, consists of an amazingly diverse assemblage that has passed under a series of names including those cited above. Saline seeps and salt marshes, streamsides, terraces, and other meadowlands at 1310 to 3175 m in Carbon, Duchesne, Emery, Garfield, Juab, Millard, Salt Lake, Sanpete, Sevier, Summit, Tooele, and Utah counties; British Columbia to Montana, south to California, Arizona, and Colorado. This phase of *C. scariosum* has passed under the names *C. acaulescens* (Gray) Schum., *C. coloradoense* (Rydb.) Cockerell; *C. tioganum* (Congdon) Petrak, *C. drummondii* T. & G., and *C. foliosum.* Nomenclature is still unclear, and more work is indicated. Our highly variable material is transitional from acaulescent to caulescent within populations, with stems, when present, that are fleshy and edible. This is our common thistle of meadowlands, and it is unfortunate that nomenclatural entanglements have not allowed selection of an unequivocal name.

Var. ***thorneae*** **Welsh var. nov.** A *C. scarioso* var. *scarioso* in capitulis majoribus et caulibus longioribus differt. Type.— USA. Utah: Piute Co., margin of Otter Creek, Grass Valley, 6.5 mi n of Angle, T28S, R1W, S30, Volcanic sediments, 2013 m elev., 11 Aug. 1976. S. L. & S. L. Welsh 14369 (Holotype BRY). Additional specimens: Utah. Beaver Co., Needle Range, Vances Spring, T28S, R18W, S17, 7 July 1976, Welsh & Holmgren 13903 (BRY); do, Wah Wah Spring, 28 Aug. 1980, Welsh et al. 20157. Garfield Co., Pine Lake, 27 July 1977. Neese & White 3830 (BRY). Iron Co., Cedar Mt., near Navajo Lake, 28 July 1971, Higgins 4669 (BRY). Kane Co., along Skutumpa Creek, T40S, R41/2W, S76, 4 Aug. 1976, Welsh et al. 14250 (BRY). Millard Co., Pavant Mts., T21S, R21/2W, S2, 15 Aug. 1978, Welsh & Henroid 18031 (BRY). Piute Co., 1 mi E of Kingston, 25 July 1964, Welsh & Moore 3352 (BRY); do, 2 mi W Kingston, 20 Aug. 1976, Welsh & Taylor 14443 (BRY). In addition to the features noted above, the cauline leaves are thick, with coarse veins, and spines 8–35 mm long; endemic.

Cirsium virginensis **Welsh sp. nov.** Virgin Thistle. Perennial(?) herbs from taproots; leaves of basal rosettes 6–35 cm long, 1–5 cm wide, unlobed, pubescent like the cauline ones, with spines 1–4 mm long; stems 6–15 dm tall, tomentose, winged by definitely decurrent leaf bases; cauline leaves 1.5–15 cm long or more, sinuate-dentate to pinnatifid, whitish tomentose on both sides, or greenish above, often reduced to spiney bracts upwards; involucres 13–20 mm tall, 12–32 mm wide, the bracts ovate-lanceolate to narrowly lanceolate, brownish to straw colored, or often suffused with purple, tomentose marginally (or overall), the outer not especially reflexed, the inner serrulate or entire, smooth medially, the glandular dorsal ridge more or less developed, the apical portions of the inner often contorted; spines 2–6 (8) mm long, yellowish; corollas pink to lavender (or white?). Saline seems and stream terraces at 850 to 950 m in Washington Co.; Arizona. The small heads and long decurrent leaf bases are diagnostic.

Ab *Circio undulato* distinguibili in foliis non lobato et alato decurrenti et capitulis parvioribus. Type.— USA. Utah: Washington Co., St. George, T42S, R15W, S19, hanging garden in sandstone cliffs, at 900 m elev, 13 June 1982, S. L. Welsh 21234 (Holotype

BRY; Isotypes NY, CAS, ISC, MO, POM, UT, UTC, RM). Additional specimens: Utah. Washington Co., St. George, 16 Sept. 1935, Galway 8470 (BRY;US); do, 30 June 1947, Galway 2214G (US); do, 3 June 1938, Galway sn (BRY); do, Higgins 17 Aug. 1947, Higgins 10998 (BRY). Washington Co., Beaverdam Mts., at jct of Hwy 91, and Gunlock Road, in field north of the road, T41S, R17W, S28, at ca 975 m elev, 19 Aug. 1966, Higgins 836. Arizona: Mohave Co., I-15 river bridge, near Littlefield, 27 Aug. 1980, Bundy 200 (BRY).

Although this handsome thistle is compared to *C. undulatum* in the diagnosis, its relationships are unknown. It does not appear to be closely related to other species in the complex groups represented in our area.

LITERATURE CITED

Moore, R. J., and C. Frankton. 1965. Cytotaxonomy of *Cirsium hookerianum* and related species. Canad. J. Bot. 43: 597–613.

Petrak, F. 1917. Die nordamerikanischen Arten der Gattung *Cirsium*. Beih. Bot. Centralbl. (Abt. 2), 35: 223–567.

A SPECIES OF *CRYPTANTHA* (BORAGINACEAE) DEDICATED TO THE MEMORY OF F. CREUTZFELDT

Stanley L. Welsh[1]

Abstract.— Described as new is *Cryptantha creutzfeldtii* Welsh, named to honor the memory of F. Creutzfeldt, botanist with the Gunnison Expedition of 1853–54, who was killed along with Gunnison and other members of the party in an Indian ambush.

During preparation of a manuscript dealing with Utah plant types and their collectors and authors, it became apparent that one of our earliest botanists has not received the attention of the botanical public. That person is known simply as F. Creutzfeldt, and little information is known about him. He was the botanist with the ill-fated Gunnison expedition of 1853–54. That expedition was involved with exploration of a feasible route for a railroad from the Mississippi River to the Pacific Ocean (Beckwith 1854). Creutzfeldt died (on 26 October 1853) along with Gunnison and other members of the party in an Indian attack while they were camped along the Sevier River, near present-day Delta. Captain John Williams Gunnison was in command of the expedition, which had been split prior to the Indian attack. Lieutenant Edward Griffin Beckwith was in charge of a portion of the expedition that was working separately from Gunnison at the time of the disaster. Beckwith was named to succeed Gunnison. Creutzfeldt had collected types of *Eriogonum corymbosum* Benth. in DC. var. *divaricatum* T. & G. in Beckwith and *E. leptocladon* T. & G. in Beckwith in the vicinity of the Green River crossing. The specimens of those taxa are deposited at NY. Plant taxa have been named after both Gunnison and Beckwith, but none have been named in honor of the memory of the one person who gave more than anyone to the cause of plant collection in Utah—his life.

Therefore, it is with humility and a sense of gratitude that I name the following plant after F. Creutzfeldt, who passed to the west, south of where this plant has existed undescribed since his time.

Cryptantha creutzfeldtii Welsh, sp. nov.

Similis *Cryptantha jonesiana* (Payson) Payson sed in folius longioribus et acutis glabris supra et acutis vel obtusis staturis elatioribus et calycibus majoribus differt.

Perennial herbs, 0.7–2.3 dm tall; stems many, arising from a multicipital caudex and stout black-barked taproot, the caudex branches 2–12 cm long clothed by marcescent leaf bases; leaves narrowly spatulate to oblanceolate, acute to obtuse, 2–8 cm long, 0.2–0.9 cm wide, coarsely appressed setose-pustulate (appearing ashy gray on leaves of previous years) below, the petioles long-setose; inflorescence an interrupted thyrse, with few to several clusters below the terminal subcapitate one; calyx segments lance-linear in anthesis, 6–8 mm long, in fruit 9–13 mm long, densely long-setose with yellowish, ascending bristles; corolla white, the tube 8–11 mm long, campanulate in the throat; the fornices low and broad, crests at base of tube lacking, the limb 10–13 mm wide; nutlets lanceolate, 4–5 mm long, muricate; scar narrow, open, without an elevated margin.

Type.— USA. Utah: Emery County, T21S, R6E, S22, ca 1.5 mi nw hwy 10, along dirt road at Muddy Creek historical marker, on slope S of canal, 6400 ft (1952 m), shadscale community, 14 May 1981, S. L. Welsh 20470 (Holotype BRY; isotypes NY, ISC, POM, CAS, MINN, COLO, RM, UT, UTC, UC, MO, and others).

---

[1] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Additional specimens: Utah, Carbon Co., T14S, R10E, S17–18, ca 1 mi W Price, ¼ mi S Castleview Hospital, Mancos Shale slope at ca 5500 ft (1678 m) elev., 19 May 1981, L. Arnold sn (BRY); NY, ISC, POM, CAS, MINN, COLO, RM, UT, UTC, UC, MO, RENO. Emery Co., T21S, R6E, S27, 5 mi SW of Muddy Creek, 3 mi N Emery, Bluegate Member, clay soil, 26 May 1979, E. Neese & S. White 7362 (BRY); Castle Dale, SE Buzzard Bench, 20 May 1976, J. Allan 762, (BRY); T22S, R6E, NE¼ S7, 1.7 mi due W Emery; 30 May 1979, S. White 15 (BRY); T21S, R6E, S28, 1.5 mi due N Emery, 7 June 1979, S. White & G. Moore 77 (BRY); T20S, R6E, S14, Ferron Canyon, 23 May 1980, N. D. Atwood 7518 (BRY); SW of Orangeville, below Buzzard Bench, 27 April 1979, J. Allan 947 (BRY).

The Creutzfeldt cryptantha is a near ally of *Cryptantha jonesiana* (Payson) Payson. Diagnostic features of the former include the acute to obtuse leaves that are glabrous above, the stature that averages taller at maturity, the larger calyces, and the large nutlets. The two taxa are spatially and edaphically isolated, with *C. jonesiana* occupying portions of the Summerville and Moenkopi formations in the central portions of the San Rafael Swell, and *C. creutzfeldtii* occurring on the Blue Gate Member of the Mancos Shale Formation along the strike of that formation below the coal measures of the Mesa Verde Group of formations. Both flower in early springtime, and each is characterized by the broad corolla limbs, vesture of pustulate-based setae, and slender accrescent calyx lobes.

Literature Cited

Higgins, L. C. 1971. A revision of *Cryptantha* subgenus Oreocarya. BYU Sci. Bull., Biol. Ser. 13 (4).

Beckwith, E. G. 1855. Reports of explorations and surveys, to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. House Rep. Exec. Doc., Vol. 2, No. 91.

ALGAL POPULATIONS IN BOTTLE HOLLOW RESERVOIR, DUCHESNE COUNTY, UTAH

Jeffrey Johansen[1], Samuel R. Rushforth[2], and Irena Kaczmarska[3]

Abstract.— Bottle Hollow Reservoir contains a diverse algal flora. A total of 289 taxa was observed, 227 of which were diatoms. Both littoral and planktonic communities had high diatom diversity. During summer months filamentous Chlorophyta were diverse and high in biomass in the littoral zone. Phytoplankton collections in Bottle Hollow Reservoir were dominated by four species: *Asterionella formosa, Cyclotella comta, Dinobryon divergens*, and *Fragilaria crotonensis*. Plankton samples contained mostly small diatoms in early spring, with larger algae succeeding these as the summer progressed. No blue-green algae were important in this succession. Two peak production periods were observed, one in the fall and one in the spring. Bottle Hollow Reservoir appears to be a healthy mesotrophic system based on the evidences of moderately high algal diversity, insignificance of blue-green algae, and the presence of a suite of diatom species indicative of mesotrophic conditions.

Bottle Hollow Reservoir is in Fort Duchesne, Duchesne County, Utah, on the Ute Indian Reservation. It was planned and constructed by the Bureau of Reclamation as a mitigation component of the Bonneville Unit of the Central Utah Project. The primary function of this reservoir was to replace part of the fisheries and recreation lost due to the construction of the Rock Creek component of the Central Utah Project. Bottle Hollow Reservoir is presently the central component of the Bottle Hollow Resort owned and operated by the Ute Indian Tribe. It is used primarily for sport fishing.

Construction of Bottle Hollow Reservoir was completed in 1971 and the lake was filled during 1972. Water for the reservoir is taken from the Uinta River through the Indian Bench Canal that originates 11 km to the northwest. Little outflow is released from the reservoir at any time of the year. Water to replace that lost by evaporation and seepage is brought from the Uinta River through the Indian Bench Canal during the early spring. No appreciable flushing or flow-through has occurred in the reservoir since its completion. Total capacity of Bottle Hollow Reservoir is 11,103 acre feet, with usable capacity at essentially the same figure. Elevation of the spillway is 1552.8 meters, and surface area of the reservoir is 418 acres.

Fishing in Bottle Hollow has been good to excellent since its completion. The fishery is based primarily upon planted brown trout (Merritt et al. 1980). Concern to maintain this fishery and concern over somewhat poorer catches during the past few years led the Ute Indian Tribe to initiate a comprehensive study of the water quality and biology of the system. This study was financed by the Environmental Protection Agency through an areawide 208 water quality planning grant. We have studied the algal floras of this reservoir during 1977 and 1979–1980.

Methods

Ten collection stations were established to monitor the plankton and attached algae in Bottle Hollow Reservoir (Fig. 1). The first five were identical to the water quality stations used by Merritt et al. (1980) for chemical and physical analyses of the reservoir. Littoral collections were made at four sites around the periphery of the reservoir: the shore near the inlet channel, the north end, the south dam, and the south end. The inlet channel itself was also sampled. Four series of collections were made during the 1979–80 study period (Table 1).

---

[1] Department of Oceanography, Texas A & M University, College Station, Texas 77843.

[2] Department of Botany, Brigham Young University, Provo, Utah 84602.

[3] Polish Academy of Sciences, Institute of Botany, Department of Phycology, ul. Lubicz 46, 31-512 Krakow, Poland.

Plankton samples were collected using a 2.3 liter capacity Van Doren bottle. Four Van Doren bottles distributed evenly through the euphotic zone were collected at each phytoplankton site and filtered through a 35 mm mesh phytoplankton net into a large bucket, yielding a composite net plankton sample for each site. In addition, a composite nannoplankton sample was collected by sampling the filtrate in the bucket. Sediment samples were collected using an Ekmann Dredge.

Littoral algal collections were chiefly of attached species, though twice unattached filamentous green algae were collected (Table 1). Attached algae consisted of epiphyton (algae growing on vascular plants), epilithon (algae attached to rocks), and epipsammon (algae growing on and in sand or silt).

Samples were returned to Brigham Young University and placed under refrigeration. Analyses of living algae were made within one week after collection. Nannoplankton samples were concentrated by vacuum filtration through Millipore filters (1.2 mm pore size). Estimates of absolute densities of planktonic algae were made using Palmer Cell water mounts. Living algae in littoral and benthic samples were identified and the abundance of each species estimated.

After living algae were studied, the diatoms in each sample were cleaned, using standard nitric acid oxidation techniques (St. Clair and Rushforth 1976), and mounted in Hyrax resin. All algae were examined and identified using Zeiss RA research microscopes with phase contrast and Nomarski interference phase accessories.

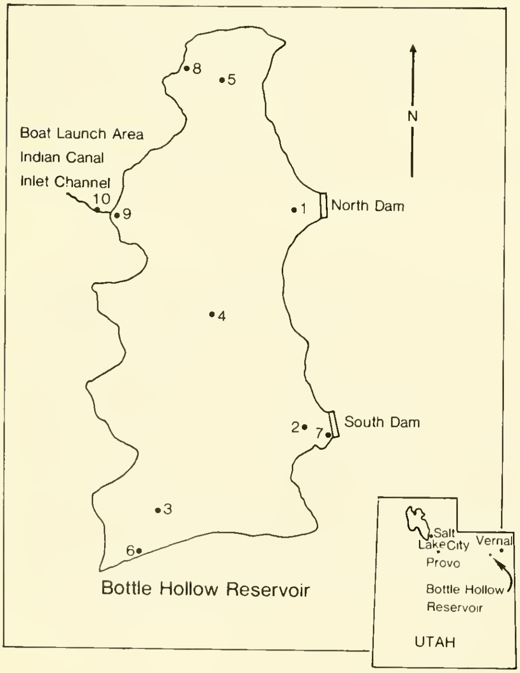


Fig. 1. Reference map of Bottle Hollow Reservoir showing the collecting localities.

Results

A total of 280 algal taxa were observed during this study. Twenty-three of these were blue-green algae (Cyanophyta); 32 were green algae (Chlorophyta); 4 were euglenophytes (Euglenophyta); 2 were dinoflagellates (Pyrrhophyta); one was a chrysophyte (Chrysophyta); and 227 were diatoms (Bacillariophyta). All algal species, together with their occurrence in the major microhabitats of the reservoir, are listed in Table 2. Living algae were not observed in any of the sediment collections, and so diatom slides made from these samples were not quantitatively analyzed.

Littoral communities were dominated by filamentous green algae most of the year. These were chiefly representatives of

Table 1. Algal samples collected from Bottle Hollow Reservoir during the 1979–1980 sampling period. All samples were examined for nondiatoms. Permanent diatom slides of samples from stations 1–6 and 9 were also examined. Key: P = plankton; S = sediments; Ep = epiphytic algae; El = epilithic algae; Es = epipsammic algae; L = littoral unattached algae.

Station	15 Nov 1979	27 Mar 1980	20 Jun 1980	26 Jul 1980
1	P, S	P, S		
2	P, S	P, S	P	P
3	P, S	P, S		
4	P, S	P, S		
5	P, S	P, S		
6	Ep, Es	Ep, Es	Ep, Es	El, Es
7	El, Es		El	El
8	El, Es, L		L	El, Es
9	Ep, Es	Ep, Es		Es
10	El		El	El

TABLE 2. Algal species collected from Bottle Hollow Reservoir, Duchesne County, Utah, with their distribution in the various habitats studied.

Species	Inflow	Benthos	Epiphyton	Epipsammon	Epilithon	Plankton
CYANOPHYTA						
Anabaena variabilis Kuetzing	x		x	x		
Anabaena sp.			x	x		
Aphanizomenon flos-aquae (Lemm.) Ralfs			x	x	x	
Calothrix sp.					x	
Chroococcus limneticus Lemmermann			x	x	x	
Chroococcus turgidus (Kg.) Naegeli						x
Gloeocapsa decorticans (A. Br.) P. Richt.				x		
Gomphosphaeria aponina var. *delicatula* Virieux				x	x	x
Lyngbya birgii G.M. Smith					x	
Lyngbya diguetii Gomont	x					
Merismopedia glauca (Ehr.) Naegeli			x			
Nodularia spumigena Mertens	x					
Oscillatoria agardhii Gomont		x	x			
Oscillatoria angusta Koppe			x	x	x	
Oscillatoria geminata Schwabe			x			
Oscillatoria limnetica Lemmermann	x			x	x	
Oscillatoria limosa (Roth) Agardh			x	x	x	
Oscillatoria subbrevis Schmidle	x			x	x	
Oscillatoria tenuis Agardh			x	x	x	
Oscillatoria sp.			x			
Phormidium tenue (Menegh.) Gomont	x		x	x	x	
Spirulina major Kuetzing				x	x	
Tolypothrix distorta Kuetzing			x			
CHLOROPHYTA						
Ankistrodesmus falcatus (Corda) Ralfs	x		x			x
Chlamydomonas globosa Snow			x		x	
Cladophora glomerata (Lemm.) Kuetzing	x		x			
Closterium dianae Ehrenberg				x		
Cosmarium nitidulum De Not.						x
Cosmarium sp.				x	x	x
Dictyosphaerium ehrenbergianum Neageli						x
Eudorina elegans Ehrenberg						x
Mougeotia sp.					x	x
Oedogonium sp. 1	x		x	x	x	
Oedogonium sp. 2			x			
Oedogonium sp. 3	x		x	x	x	
Oedogonium sp. 4			x	x	x	
Oedogonium sp. 5	x		x	x	x	x
Oedogonium sp. 6	x					
Oocystis gloeocystiformis Borge						x
Oocystis pusilla Hansgirg			x			
Pediastrum boryanum (Turp.) Meneghini						x
Rhizoclonium hieroglyphicum (Ag.) Kuetzing	x		x	x	x	
Rhizoclonium sp.			x			
Scenedesmus bijuga (Turp.) Lagerheim						x
Scenedesmus quadricauda var. *longispina* (Chod.) G.M. Smith				x		
Scenedesmus quadricauda var. *quadrispina* (Turp.) Brebisson					x	
Sphaerocystis schroeteri Chodat						x
Spirogyra sp. 1				x	x	
Spirogyra sp. 2			x	x		
Spirogyra sp. 3			x	x	x	
Spirogyra sp. 4			x	x	x	
Spirogyra sp. 5	x		x	x	x	x

Table 2 continued.

Species	Inflow	Benthos	Epiphyton	Epipsammon	Epilithon	Plankton
Staurastrum gracile(?) Ralfs						x
Ulothrix zonata (Weber et Mohr) Kuetzing	x			x		
Zygnema sp.			x	x		
EUGLENOPHYTA						
Euglena elastica Prescott				x		
Euglena gracilis Klebs			x			x
Trachelomonas abrupta (Swir.) Deflandre			x			x
Trachelomonas dybowskii Drezepolski			x			x
PYRRHOPHYTA						
Ceratium hirudinella (O.F. Muell.) Dujardin						x
Glenodinium pulvisculus (Ehr.) Stein				x	x	
CHRYSOPHYTA						
Dinobryon divergens Imhof			x	x	x	x
BACILLARIOPHYTA						
Achnanthes clevei Grunow			x	x		x
Achnanthes conspicua A. Mayer				x		x
Achnanthes exigua Grunow			x	x	x	x
Achnanthes gibberula Grunow						x
Achnanthes hauckiana Grunow			x	x	x	x
Achnanthes kryophila Petersen			x			x
Achnanthes lanceolata (Breb.) Grunow			x	x	x	x
Achnanthes lanceolata var. *dubia* Grunow			x	x		
Achnanthes linearis (W.Sm.) Grunow			x	x	x	x
Achnanthes linearis f. *curta* H.L. Smith						x
Achnanthes minutissima Kuetzing			x	x	x	x
Achnanthes orientalis Hustedt						x
Achnanthes peragalli var. *fossilis* Tempere & Peragallo				x		
Achnanthes sp. 1			x			x
Achnanthes sp. 2			x			x
Amphipleura pellucida Kuetzing				x		
Amphora coffeiformis (Ag.) Kuetzing			x	x		x
Amphora ovalis (Kg.) Kuetzing				x		x
Amphora ovalis var. *affinis* (Kg.) v. Heurck ex De Toni						x
Amphora ovalis var. *pediculus* (Kg.) v. Heurck ex De Toni				x	x	x
Amphora perpusilla (Grun.) Grunow			x	x	x	x
Amphora veneta Kuetzing			x	x	x	x
Anomoeoneis serians (Breb. ex Kg.) Cleve			x			
Anomoeoneis serians var. *brachysira* (Breb. ex Kg.) Hustedt						x
Anomoeoneis sphaerophora (Kg.) Pfitzer						x
Anomoeoneis zellensis (Grun.) Cleve			x	x		
Asterionella formosa Hassall			x	x		x
Bacillaria paxillifer (O. Muell.) Hendey						x
Biddulphia levis Ehrenberg						x
Caloneis amphisbaena (Bory) Cleve					x	
Caloneis bacillum (Grun.) Cleve			x	x	x	x
Caloneis lewisii Patrick			x	x	x	x
Caloneis lewisii var. *inflata* (Schultze) Patrick			x	x		x
Caloneis ventricosa var. *truncatula* (Grun.) Meister			x			x
Chaetoceros sp.						x
Cocconeis pediculus Ehrenberg			x	x		
Cocconeis placentula Ehrenberg			x			

Table 2 continued.

Species	Inflow	Benthos	Epiphyton	Epipsammon	Epilithon	Plankton
Cocconeis placentula var. *euglypta* (Ehr.) Cleve			x			
Cocconeis placentula var. *lineata* (Ehr.) Cleve	x	x				x
Cyclotella caspia Grunow						x
Cyclotella comta (Ehr.) Kuetzing	x	x	x			x
Cyclotella meneghiniana Kuetzing						x
Cyclotella sp.						x
Cylindrotheca gracilis (Breb.) Grunow	x	x	x			x
Cymatopleura solea (Breb.) W. Smith	x					x
Cymbella affinis Kuetzing	x	x				x
Cymbella brehmii Hustedt	x	x				x
Cymbella cuspidata Kuetzing	x					
Cymbella cymbiformis Agardh	x	x	x			
Cymbella mexicana (Ehr.) Cleve		x				x
Cymbella microcephala Grunow	x	x	x			x
Cymbella minuta Hilse ex Rabenhorst	x					
Cymbella minuta var. *latens* (Krasske) Reimer	x					
Cymbella minuta var. *silesiaca* (Bleisch ex Rabh.) Reimer	x	x	x			
Cymbella muelleri Hustedt	x	x				
Cymbella norvegica Grunow		x				
Cymbella sinuata Gregory	x	x				x
Cymbella tumida (Breb.) v. Heurck	x					
Cymbella turgidula Grunow		x				
Cymbella sp. 1						x
Cymbella sp. 2	x	x				
Denticula elegans f. *valida* Pedicino		x				
Denticula sp.	x	x	x			
Diatoma tenue Agardh	x	x				x
Diatoma tenue var. *elongatum* Lyngbye	x					x
Diploneis oculata (Breb.) Cleve	x					x
Diploneis subovalis Cleve	x	x	x			x
Entomoneis ornata (Bail.) Reimer		x				
Epithemia adnata var. *proboscidea* (Kg.) Patrick	x	x	x			x
Epithemia argus var. *protracta* A. Mayer						x
Epithemia smithii Carruthers	x	x	x			
Epithemia sorex Kuetzing	x	x	x			x
Epithemia turgida (Ehr.) Kuetzing	x	x				x
Fragilaria brevistriata Grunow	x					
Fragilaria brevistriata var. *inflata* (Pant.) Hustedt	x	x	x			x
Fragilaria cf *capucina* Desmazieres	x	x				
Fragilaria capucina var. *mesolepta* Rabenhorst	x					
Fragilaria construens var. *venter* (Ehr.) Grunow		x				x
Fragilaria crotonensis Kitton	x	x	x			x
Fragilaria crotonensis var. *oregonica* Sovereign	x					x
Fragilaria leptostauron (Ehr.) Hustedt	x	x				x
Fragilaria leptostauron var. *dubia* (Grun.) Hustedt	x	x	x			
Fragilaria pinnata Ehrenberg	x	x	x			x
Fragilaria similis Krasske						x
Fragilaria vaucheriae (Kg.) Peterson	x	x	x			x
Fragilaria virescens Ralfs	x					x
Frustulia vulgaris (Thw.) De Toni		x				
Gomphonema acuminatum Ehrenberg	x					
Gomphonema affine Kuetzing	x					
Gomphonema dichotomum Kuetzing	x					
Gomphonema instabilis Hohn & Hellerman	x	x				x
Gomphonema intricatum Kuetzing	x					

Table 2 continued.

Species	Inflow	Benthos	Epiphyton	Epipsammon	Epilithon	Plankton
Gomphonema olivaceum (Lyngb.) Kuetzing	x					x
Gomphonema olivaceum var. *calcarea* (Cl.) Cleve	x					
Gomphonema parvulum Kuetzing	x	x				x
Gomphonema parvulum var. *micropus* (Kg.) Cleve	x	x				x
Gomphonema subclavatum (Grun.) Grunow	x	x				
Gomphonema truncatum Ehrenberg	x					
Gomphonema sp.	x					
Gyrosigma acuminatum (Kg.) Rabenhorst	x	x	x			x
Gyrosigma fasciola (Ehr.) Griffith & Henfrey						x
Gyrosigma obtusatum (Sulliv. & Wormley) Boyer	x	x	x			
Hannaea arcus (Ehr.) Patrick	x					
Hantzschia amphioxys (Ehr.) Grunow						x
Hantzschia distincte-punctata (Hust.) Hustedt	x					x
Hantzschia virgata (Roper) Grunow	x					
Mastogloia braunii Grunow						x
Mastogloia smithii var. *lacustris* Grunow	x	x	x			x
Melosira granulata (Ehr.) Ralfs						x
Navicula anglica Ralfs						x
Navicula anglica var. *subsalsa* (Grun.) Cleve	x	x	x			x
Navicula arvensis Hustedt	x	x	x			x
Navicula atomus (Kg.) Grunow	x					
Navicula bacilliformis Grunow						x
Navicula capitata Ehrenberg	x					x
Navicula capitata var. *hungarica* (Grun.) Ross		x				x
Navicula capitata var. *lunebergensis* (Grun.) Patrick		x				x
Navicula cincta (Ehr.) Ralfs						x
Navicula circumtexta Meister ex Hustedt		x				x
Navicula clementoides Hustedt		x				
Navicula contenta f. *biceps* (Arnot.) Grunow						x
Navicula cryptocephala Kuetzing		x				
Navicula cryptocephala var. *exilis* (Kg.) Grunow						x
Navicula cryptocephala var. *veneta* (Kg.) Rabenhorst	x	x	x			x
Navicula cuspidata (Kg.) Kuetzing	x	x				
Navicula decussis Oestrup	x	x				x
Navicula disjuncta Hustedt		x				x
Navicula elginensis (Greg). Ralfs			x			
Navicula exigua var. *capitata* Patrick		x				
Navicula gastrum Ehrenberg		x				x
Navicula graciloides A. Mayer						x
Navicula grimmei Krasske		x				x
Navicula halophila (Grun.) Cleve						x
Navicula halophila f. *tenuirostris* Hustedt		x				x
Navicula heufleri Grunow		x				
Navicula heufleri var. *leptocephala* (Breb. ex Grun.) Patrick	x	x	x			x
Navicula luzonensis Hustedt	x	x				
Navicula menisculus var. *upsaliensis* (Grun.) Grunow	x	x	x			x
Navicula minima Grunow		x	x			x
Navicula mutica var. *cohnii* (Hilse) Grunow	x	x	x			x
Navicula mutica var. *undulata* (Hilse) Grunow	x	x				
Navicula oblonga Kuetzing						x
Navicula pelliculosa (Breb. ex Kg.) Hilse	x	x	x			x
Navicula peregrina (Ehr.) Kuetzing	x	x				
Navicula permitis Hustedt	x	x				x
Navicula pupula Kuetzing	x	x	x			x
Navicula pupula var. *mutata* (Krasske) Hustedt	x					

Table 2 continued.

Species	Inflow	Benthos	Epiphyton	Epipsammon	Epilithon	Plankton
Navicula pupula var. *rectangularis* (Greg.) Grunow	x	x				
Navicula pygmaea Kuetzing						x
Navicula radiosa Kuetzing	x	x				
Navicula radiosa var. *tenella* (Breb. ex Kg.) Grunow	x	x				x
Navicula rhynchocephala Kuetzing		x				
Navicula salinarum var. *intermedia* (Grun.) Cleve	x	x	x			x
Navicula secreta var. *apiculata* Patrick	x	x	x			x
Navicula tantula Hustedt	x	x				x
Navicula tenelloides Hustedt						x
Navicula tenera Hustedt	x	x	x			x
Navicula tripunctata (Muehl.) Bory						x
Navicula tripunctata var. *schizonemoides* (v. Heurck) Patrick	x	x	x			x
Navicula viridula (Kg.) Kuetzing			x			
Navicula viridula var. *linearis* Hustedt		x				
Navicula viridula var. *rostellata* (Kg.?) Cleve		x				x
Navicula sp. 1						x
Navicula sp. 2	x	x				x
Navicula sp. 3						x
Navicula sp. 4		x				
Navicula sp. 5		x				
Navicula sp. 6			x			
Neidium bisulcatum var. *baicalense* (Skr. & Meyer) Reimer		x				
Neidium dubium (Ehr.) Cleve	x	x				x
Nitzschia acicularis W. Smith	x					
Nitzschia acicularoides Hustedt	x					x
Nitzschia cf *amphibia* Grunow	x					x
Nitzschia angustata (W. Sm.) Grunow	x	x	x			x
Nitzschia apiculata (Greg.) Grunow			x			
Nitzschia circumsuta (?) (Bail.) Grunow						x
Nitzschia dissipata (Kg.) Grunow	x	x	x			x
Nitzschia frustulum Kuetzing	x	x				x
Nitzschia gandersheimensis Krasske		x	x			x
Nitzschia hantzschiana Rabenhorst	x	x	x			x
Nitzschia hungarica Grunow		x				x
Nitzschia inconspicua Grunow	x	x	x			x
Nitzschia microcephala Grunow	x	x	x			x
Nitzschia minutula Grunow	x	x	x			x
Nitzschia ovalis Arnott	x	x				x
Nitzschia palea (Kg.) W. Smith	x	x	x			x
Nitzschia paleacea Grunow	x	x	x			x
Nitzschia punctata (W. Sm.) Grunow	x					
Nitzschia pusilla (Kg.) Grun. em. Lange-Bertalot	x	x	x			x
Nitzschia recta Hantzsch	x	x	x			x
Nitzschia romana Grunow	x	x				x
Nitzschia sigma var. *sigmatella* Grunow		x				x
Nitzschia sigmoidea (Ehr.) W. Smith	x	x				x
Nitzschia sinuata (W. Sm.) Grunow						x
Nitzschia sinuata var. *tabellaria* Grunow	x	x	x			
Nitzschia sociabilis Hustedt						x
Nitzschia trybionella var. *debilis* (Arnott) A. Mayer		x				x
Nitzschia trybionella cf var. *levidensis* (W. Sm.) Grunow						x
Nitzschia trybionella var. *victoriae* Grunow						x
Nitzschia valdestriata Aleem & Hustedt	x	x	x			
Nitzschia sp. 1	x	x	x			x
Nitzschia sp. 2	x	x				x

Table 2 continued.

Species	Inflow	Benthos	Epiphyton	Epipsammon	Epilithon	Plankton
Pinnularia abaujensis var. *linearis* (Hust.) Patrick	x					
Pinnularia borealis Ehrenberg			x			
Pinnularia brebissonii Kuetzing	x					
Pinnularia brebissonii var. *diminuta* (Grun.) Cleve.						x
Pleurosigma sp.		x				
Rhoicosphenia curvata (Kg.) Grunow		x				x
Rhopalodia gibba (Ehr.) O. Mueller	x	x				x
Rhopalodia gibberula (Ehr.) O. Mueller		x				
Rhopalodia gibberula var. *vanheurckii* O. Mueller	x	x	x			x
Stauroneis anceps Ehrenberg	x					
Stauroneis smithii Grunow		x				
Stauroneis cf *smithii* Grunow						x
Stauroneis wislouchii Por. et Anisim.	x	x	x			x
Stephanodiscus astraea var. *minutula* (Kg.) Grunow						x
Stephanodiscus niagarae Ehrenberg						x
Stephanodiscus sp.						x
Surirella angusta Kuetzing		x				
Surirella ovalis Brebisson	x	x				x
Synedra acus Kuetzing	x	x				x
Synedra cyclopum Brutschi						x
Synedra fasciculata (Ag.) Kuetzing	x	x				x
Synedra fasciculata var. *truncata* (Grev.) Patrick						x
Synedra pulchella Kuetzing	x		x			x
Synedra radians Kuetzing	x					
Synedra ulna (Nitzsch) Ehrenberg	x	x				x
Synedra ulna var. *ramesi* (Herib. et Perag.) Hustedt		x				

Zygnematales (*Spirogyra*, *Mougeotia*, and *Zygnema* species), though *Oedogonium* species were also important. Because sexual stages were not observed, these taxa could not be identified beyond the generic level. *Cladophora glomerata* was important in the inlet channel but was also occasionally common in some littoral sites of the reservoir. *Ulothrix zonata* was abundant in the channel in November, but was only rarely observed in the reservoir. Diatoms were also important in the littoral communities, and dominated the algal assemblage during the winter and early spring. Filamentous Chlorophyta died off during the winter and were not reestablished until early summer. Diatoms on the other hand recovered soon after winter ice had melted. The eight most important diatoms in the littoral sites were all pennate species; *Diatoma tenue, Fragilaria vaucheriae, Gomphonema instabilis, Navicula cryptocephala* var. *veneta*, *Navicula mutica* var. *cohnii*, *Nitzschia minutula*, *Nitzschia palea*, and *Nitzschia paleacea* (Table 3).

The three different substrata sampled showed differences in diatom floras. *Cocconeis placentula* var. *lineata*, *Cymbella minuta* var. *silesiaca*, *Gomphonema olivaceum*, and *Gomphonema instabilis* were primarily epiphytes. The epipsammon was characterized by small raphoid diatoms, particularly *Navicula mutica* var. *cohnii*. Filamentous green algae were either unattached or part of the epilithon and epiphyton. Most algal species in the littoral were at least to some degree cosmopolitan.

Many algal species are opportunistic generalists (Lowe 1974, Patrick and Reimer 1966). *Achnanthes minutissima*, *Navicula cryptocephala* var. *veneta*, *Nitzschia palea*, and *Nitzschia paleacea*, as well as several other small raphoid diatom species in the study, are such taxa. These organisms occur in a wide variety of habitats in western North America and worldwide (Camburn et al. 1978, Foged 1959, 1974, Hustedt 1930, 1949, Patrick and Reimer 1966). Other diatoms are best suited to grow in more specialized environments. For example, many species in the genus *Cocconeis* grow optimally on submerged macrophytes (Lowe 1974, Patrick and Reimer 1966). These species can also be found on rocks or wood and, through mixing processes in the lake, will also occur in the epipsammon and plankton. Because species are not confined to the substrate on which they are best suited, characterizing species according to habitat preference is often difficult. Even so, the planktonic algal assemblages in Bottle Hollow Reservoir were distinctly different from those of the littoral, despite the overlap of some species. The dominant algal plankters were limited to three diatom taxa and one chrysophyte; *Asterionella formosa*, *Cyclotella comta*, *Fragilaria crotonensis*, and *Dinobryon divergens* (Table 3). These species usually composed about 80 percent of the total planktonic flora. Because of this, diversity was much lower in the plankton than in the periphyton. Total phytoplankton abundance ranged from an average density as low as 700,000 organisms per liter in late July to a high of 1,700,000 organisms per liter in November.

DISCUSSION

Three areas of interest concerning the floras of Bottle Hollow Reservoir will be discussed; floristic diversity, community dynamics, and trophic condition. It has already been noted that diversity in the planktonic environment was depressed by the dominance of four algal taxa. Even so, a total of 174 algal taxa (154 of which were diatoms) were found in the phytoplankton samples. This is 60 species fewer than found in the littoral zone, which had a total of 234 taxa (184 of which were diatoms). The diversity in phytoplankton was due primarily to the infrequent occurrence of small diatom species in the water column. These species are easily transferred from the littoral and benthic areas, where they are often most common, to the open water of the lake by natural mixing processes. A few supposed littoral species such as *Achnanthes orientalis* were more common in the plankton than in the littoral collections, but these were more the exception than the rule. Because the majority of the littoral-planktonic diatoms were small, they were found primarily in nannoplankton samples and were much less frequent in the netplankton. Netplankton samples had an average of 16 diatom taxa per sample, whereas nannoplankton collections contained an average of 30 taxa (Table 4). Littoral collections contained substantially greater numbers of species. This is to be expected because the littoral environment is more heterogenous than the planktonic habitat and contains more ecological niches. The highest number of species per sample was found in the November littoral collections (Table 4).

TABLE 3. Average percent densities of the 14 most important diatom taxa in Bottle Hollow Reservoir. Average densities were computed separately for plankton and littoral samples.

Species	Plankton	Littoral
Achnanthes minutissima	.3	2.5
Asterionella formosa	25.5	.4
Cyclotella comta	17.1	.7
Cymbella microcephala	.2	2.2
Diatoma tenue	.4	3.8
Fragilaria crotonensis	39.5	1.6
Fragilaria vaucheriae	.1	3.1
Gomphonema instabilis	.1	3.9
Navicula cryptocephala var. *veneta*	.4	8.4
Navicula mutica var. *cohnii*	.1	7.9
Nitzschia microcephala	.2	2.1
Nitzschia minutula	.1	3.2
Nitzschia palea	2.1	3.8
Nitzschia paleacea	2.7	4.8

Population dynamics of the plankton are easier to monitor than those for the littoral areas. This is largely due to the relative ease of obtaining quantitative phytoplankton data versus quantitative data for attached species. If the numbers of netplankton individuals per liter are added to the numbers of nannoplankton individuals per liter from the same locality, estimates of total phytoplankton per liter of lake water are obtained. Average densities of the four most abundant taxa were computed using these estimates and plotted against time (Fig. 2). *Fragilaria crotonensis* was the most abundant species, reaching higher concentrations as the seasons progressed. The highest density of this taxon was observed in the November 1979 collections.

Several observations and speculations can be made after consideration of the data shown in Figure 2. Two periods of peak algal production, fall and spring, occur in Bottle

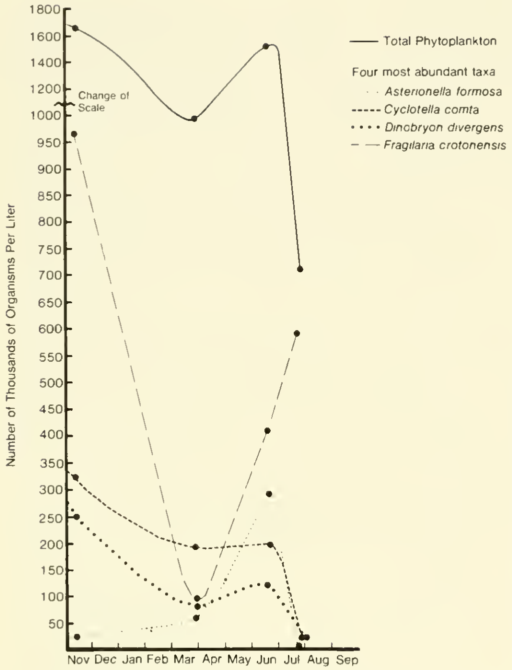


Fig. 2. Densities of the dominant phytoplankters and total phytoplankton through the 1979–1980 collecting year in Bottle Hollow Reservoir.

Hollow Reservoir. These are likely due to fall and spring turnover. During winter, production falls drastically with shorter days and ice coverage. As soon as the ice melts, small diatoms grow quickly in the recently mixed, nutrient-rich water. The March collections had substantial numbers of these small diatoms, even though the biomass was still quite low. *Cyclotella comta* was present in higher numbers than *F. crotonensis* at this time.

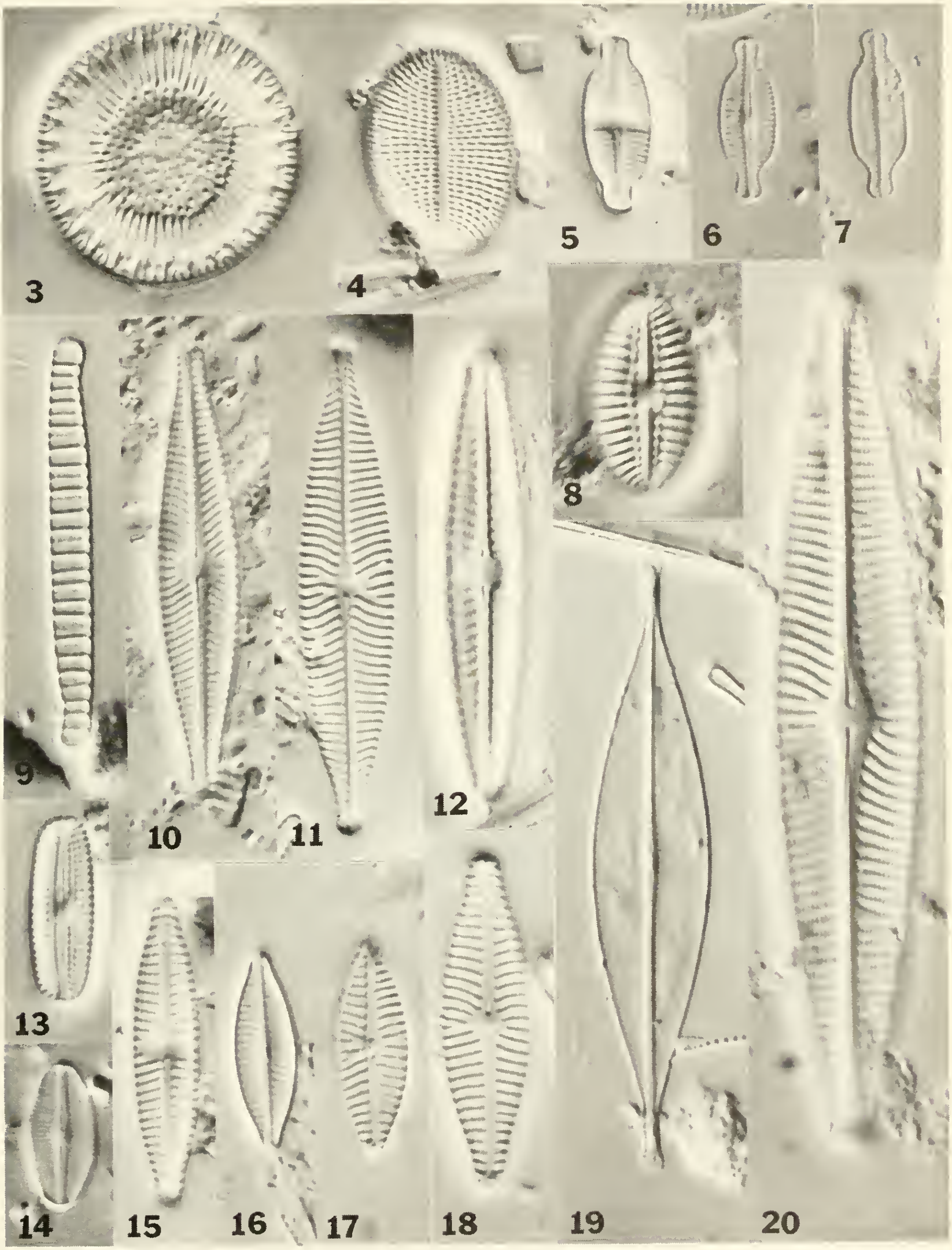
The pulse of these small algae favors the growth of small filter-feeder zooplankton (Porter 1977), such as the cladocerans that were observed in both the March and June net hauls. As the zooplankters apply a selective pressure on small diatoms, larger (often colonial) algae may become more prevalent (Porter 1977, Wimpenny 1973). The density of *Cyclotella comta* in Bottle Hollow Reservoir leveled off in June and dropped drastically in July. The larger colonial forms *Asterionella formosa, Dinobryon divergens,* and *Fragilaria crotonensis* increased in late spring and dominated the spring peak.

As summer progressed, total phytoplankton density dropped, though *F. crotonensis* continued to increase in number. This may be due to two factors. First, the lake begins to stratify during early spring, causing mixing to cease. Nutrients tied up in the living algae and zooplankton are lost to the sediments as these organisms die and sink and as feces of zooplankton and fish settle (Wetzel 1975). Second, grazing pressure may decrease total phytoplankton density as zooplankton populations reach maturity (Porter 1977). Filter-feeders cannot feed well on the large *Fragilaria* colonies, and so *F. crotonensis* tends to escape predation and continues to increase in number. An unexplained phenomena is the decrease in the large colonial algae *Asterionella formosa* and *Dinobryon divergens,* which should also have the same size refuge from filter feeders as *F. crotonensis.* The decline of *A. formosa* in early summer is a common occurrence that has been attributed to nutrient depletion in the upper water (Pearsall 1932). Another possibility is that larger raptorian-feeder zooplankton, such as many copepods, which begin to reach maturity later in summer, may have a preference for these algae over *F. crotonensis.* Finally, it is clear that either or both of these algae could decrease due to temperature increase or some other environmental factor.

Littoral algal succession was less well defined. Diatoms were particularly important in early spring and grew to some extent when the lake was covered with ice. As the water warmed, filamentous green algae became important and had the highest standing crop. Despite the higher biomass of these green algae, diatoms may be more critical to littoral

Table 4. Average number of diatom species per microhabitat type.

Microhabitat	November	March	June	July	Average
Netplankton	18.4	12.4	22.0		16.0
Nannoplankton	18.2	40.4	21.0	51.0	30.4
Epiphyton	75.5	46.5	62.0		61.2
Epipsammon	63.5	21.5	48.0	64.0	50.9

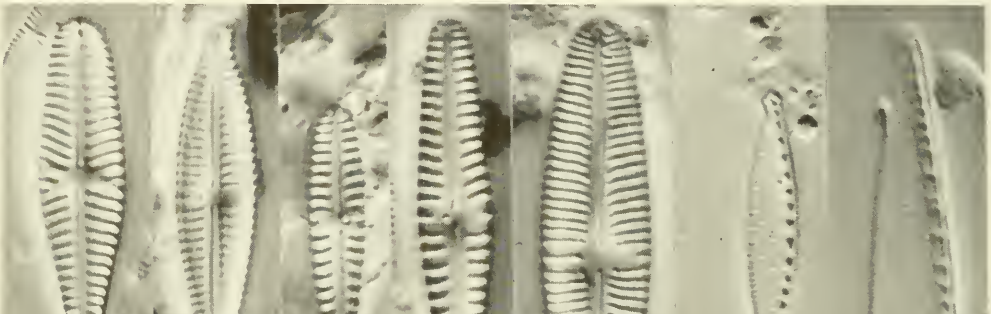


Figs. 3–20. Diatom spp.: 3, *Cyclotella comta*, 19 mm diameter, 12 striae/10 mm; 4, *Cocconeis placentula* var. *lineata*, 15 × 11 mm, 19 striae/10 mm; 5, *Achnanthes exigua*, 12.5 × 5 mm, 24 striae/10 mm; 6, *A. orientalis*, Raphe valve: 11.5 × 4 mm, 26–30 striae/10 mm; 7, *A. orientalis*, Rapheless valve: 12 × 4 mm, 26–30 striae/10 mm; 8, *Diploneis subovalis*, 14 × 8.5 mm, 11 costae/10 mm; 9, *Diatoma tenue*, 29 × 3 mm, 7–10 costae/10 mm; 10, *Navicula cryptocephala*, 32 × 6 mm, 15–18 striae/10 mm; 11, *N. salinarum* var. *intermedia*, 35 × 7 mm, 14–16 striae/10 mm; 12, *N. tripunctata*, 32 × 6 mm, 12–14 striae/10 mm; 13, *N. tenera*, 13 × 4.5 mm, 20 striae/10 mm; 14, *N.* sp. 3, 10 × 5 mm, 30 striae/10 mm; 15, *N. cryptocephala* var. *veneta* (?), 22 × 5 mm, 14–16 striae/10 mm; 16, *N. cryptocephala* var. *exilis*, 14 × 4.5 mm, 20 striae/10 mm; 17, *N. cryptocephala* var. *veneta*, 15 × 5.5 mm, 14–15 striae/10 mm; 18, *N. cryptocephala* var. *veneta*, 24 × 7 mm, 13–14 striae/10 mm; 19, *N. halophila* f. *tenuirostris*, 43 × 8.5 mm, 26 striae/10 mm; 20, *N. radiosa*, 60 × 11 mm, 9–12 striae/10 mm. All photographs are 2000X.

food webs. The annual production of the diatoms may exceed the production of the other algae because of their faster growth rates. The higher production of diatoms is not readily evident because grazers often keep their biomass low (Minshall 1978).

Interactions between the littoral and planktonic communities exist, though the extent of this interaction is difficult to assess. Planktonic species were found in the periphyton, and many littoral raphoid pennate diatoms occurred commonly in the plankton. Most freshwater phytoplankton are thought to have a neritic phase in which they dwell on the bottom, often in a resting stage (Patrick and Reimer 1966). This neritic phase would partly explain the occurrence of phytoplankton in near shore areas, though drift and settling are also factors. Likewise, many attached algae may become unattached and drift with the plankton, which could be adaptive by helping increase their distribution.

The data collected during this study indicate that Bottle Hollow Reservoir is a mesotrophic to mesotrophic-eutrophic body of water. There are several evidences for this conclusion. First, biotic diversity is higher than in most eutrophic systems in the same region but lower than in many oligotrophic systems. The littoral samples with high num bers of species and absence of dominants indicate fairly unpolluted waters. Second, the successional pattern is not characteristic of



Figs. 21–31. Diatom spp.: 21, *Gomphonema olivaceum*, 23 × 6 mm, 13–15 striae/10 mm; 22, *Gomphonema parvulum*, 24 × 5.5 mm, 14–16 striae/10 mm; 23, *G. intricatum*, 17 × 4 mm, 12–13 striae/10 mm; 24, *G. intricatum*, 28 × 5 mm, 10–14 striae/10 mm; 25, *G. instabilis*, 34 × 7 mm, 12–18 striae/10 mm; 26, *Nitzschia romana*, 20 × 3.5 mm, 26 striae/10 mm, 9–10 fibulae/10 mm; 27, *Amphora perpusilla*, 11 × 3 mm, 19 striae/10 mm; 28, *Cymbella microcephala*, 15 × 4.5 mm, 26–27 striae/10 mm; 29, *Nitzschia valdestriata*, 10 × 2.5 mm, 10 striae/10 mm, 10 fibulae/10 mm; 30, *N. sinuata* var. *tabellaria*, 18 × 7 mm, 20 striae/10 mm, 5–6 fibulae/10 mm, 31, *N. recta*, 52 × 6 mm, 7–9 fibulae/10 mm. All photographs are 2000X.

eutrophic waters because blue-green algae do not play an important role. In the plankton of most eutrophic lakes and reservoirs of temperate regions, the large diatoms and chrysophytes are succeeded by blue-green species in late summer, particularly *Aphanizomenon flos-aquae* and species of *Anabaena* (Wetzel 1975, Whiting et al. 1978). Such succession to Cyanophyta did not occur in Bottle Hollow Reservoir. Blue-green algae were also an insignificant part of the periphyton. Third, most diatoms we encountered (some of which are used as water quality indicators), were typical of mesotrophic waters. The two dominants, *Asterionella formosa* and *Fragilaria crotonensis*, are considered indicative of mesotrophic to eutrophic water (Lowe 1974, Wetzel 1975). It should be mentioned that several species we collected often indicate eutrophic water, specifically *Fragilaria vaucheriae, Navicula cryptocephala* var. *veneta, Nitzschia minutula, Nitzschia palea*, and *Nitzschia paleacea* (Lowe 1974). Nevertheless, we have observed in our studies that these are opportunistic species that occur throughout western North America in a wide variety of habitats (Anderson and Rushforth 1976, Benson and Rushforth 1975, Johansen and Rushforth 1981, Lawson and Rushforth 1975, St. Clair and Rushforth 1976, 1978). When these species dominate a system to the exclusion of more mesotrophic organisms, they provide important evidence for eutrophy. When they are present in lower numbers, together with high numbers of other algal species (conditions we found in Bottle Hollow Reservoir) they do not necessarily indicate eutrophic conditions.

The fourth confirmation of mesotrophic to mesotrophic-eutrophic water is the assemblage of saprobic indicator diatoms. The saprobien spectrum was first proposed by Kolkwitz and Marsson (1908) and is a tool for assessing water quality with respect to organic loading and pollution. All diatoms in Bottle Hollow Reservoir were checked against Lowe (1974). There were 23 mesosaprobic taxa, 28 oligosaprobic taxa, 12 saproxenous taxa, and one saprophobic species. This assemblage is evidence for water that often has a moderate to high amount of dissolved organic nutrients. It also indicates, however, that there are periods when oxidation is complete and water is quite "clean." Using Lowe (1974), it was also discovered that the majority of the diatoms are alkaliphilous.

Our studies of Bottle Hollow Reservoir have shown that the biological water quality of this body of water is quite good, particularly when compared to eutrophic systems in the same region. Even so, because of the high amounts of nutrients found naturally in the rocks of the drainage basins of eastern Utah, care must be taken to limit the human-caused introduction of pollutants into this system. We believe Bottle Hollow Reservoir has the potential to maintain a healthy fishery but also has the potential for rapid deterioration toward eutrophy.

LITERATURE CITED

ANDERSON, D. C., AND S. R. RUSHFORTH. 1976. The cryptogamic flora of desert soil crusts in southern Utah, USA. Nova Hedwigia 28:691–729.

BENSON, C. E., AND S. R. RUSHFORTH. 1975. The algal flora of Huntington Canyon, Utah, USA. Bibliotheca Phycologica 18:1–177.

CAMBURN, K. E., R. L. LOWE, AND D. L. STONEBURNER. 1978. The haptobenthic diatom flora of Long Branch Creek, South Carolina. Nova Hedwigia 30:149–279.

FOGED, N. 1959. Diatoms from Afghanistan. Biol. Skr. Det Kongl. Dan. Vid. Selsk. 11(1):1–95.

_____. 1974. Freshwater diatoms in Iceland. Bibliotheca Phycologica 15:1–118.

HUSTEDT, F. 1930. Bacillariophyta (Diatomeae). *In* A. Pascher, Die Susswasser-Flora Mitteleuropas, Heft 10, Gustav Fisher, Jena, Germany. 468 pp.

_____. 1949. Susswasser-Diatomeen aus dem Albert-Nationalpark in Belgisch-Kongo. Exploration du Parc National Albert, Mission H. Damas (1935–1936) 8:1–199. Inst. Parcs Nat. Congo Belge, Hayez, Bruxelles.

JOHANSEN, J. R., AND S. R. RUSHFORTH. 1981. Diatoms of surface waters and soils of selected oil shale lease areas of eastern Utah, USA. Nova Hedwigia 34:333–389.

KOLKWITZ, R., AND M. MARSSON. 1908. Okologie der pflanzlichen Saprobien. Ber. Deut. Bot. Ges. 26:505–519.

LAWSON, L. L., AND S. R. RUSHFORTH. 1975. The diatom flora of the Provo River, Utah, USA. Bibliotheca Phycologica 17:1–149.

LOWE, R. L. 1974. Environmental requirements and pollution tolerance of freshwater diatoms. Environmental Monitoring Series, U.S. Environmental Protection Agency. Report No. EPA-670/4-74-005. 334 pp.

MERRITT, L., S. RUSHFORTH, J. JOHANSEN, R. HECKMAN, R. WINGET, AND W. BRIMHALL. 1980. Assessment of water quality in Bottle Hollow Reservoir. Report to Ute Indian Tribe, Duchesne Co., Ut. 180 pp.

Minshall, G. W. 1978. Autotrophy in stream ecosystems. BioScience 28(12):767–771.

Patrick, R., and C. W. Reimer. 1966. The diatoms of the United States, I. Acad. Nat. Sci. Philad. Mon. 13. 1–688 pp.

Pearsall, W. H. 1932. Phytoplankton in the English Lakes. II. The composition of the phytoplankton in relation to dissolved substances. J. Ecology 20(2):241–262.

Porter, K. G. 1977. The plant-animal interface in freshwater ecosystems. Am. Scientist 65:159–170.

St. Clair, L. L., and S. R. Rushforth. 1976. The diatoms of Timpanogos Cave National Monument, Utah. Amer. J. Bot. 63(1):49–59.

______. 1978. The diatom flora of the Goshen Playa and wet meadow. Nova Hedwigia 29:191–229.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Company, Philadelphia, Penn. 743 pp.

Whiting, M. C., J. D. Brotherson, and S. R. Rushforth. 1978. Environmental interaction in summer algal communities of Utah Lake. Great Basin Nat. 38(1):31–41.

Wimpenny, R. S. 1973. The size of diatoms. V. The effect of animal grazing. J. Mar. Bio. Assoc. United Kingdom 53:957–974.

HERPETOLOGICAL NOTES FROM THE NEVADA TEST SITE

Wilmer W. Tanner[1]

Abstract.— During the years 1965–1971, considerable data were gathered that included information concerning species not previously reported. These included *Chionactis occipatalis talpina, Coleonyx variegatus utahensis, Crotaphytus collaris bicinctores, Cnemidophorus tigris tigris,* and *Sauromalus obesus obesus.* Although complete information concerning their life histories is not reported, some information concerning growth and reproduction is included.

The following notes were made by Mr. Ronald L. Morris, Dr. John E. Krogh, or the author and represent our findings concerning species found in our NTS study plots not reported previously. Several of our study plots provided some data on species that were not intensively studied or the limited data did not seemingly justify, at that time, consideration. It was our intent to gather additional data; however, this was not possible, and I am, therefore, presenting those data which are considered to have value.

Study plots were originally established for the express purpose of examining in as much detail as possible the life histories and habitats of the more abundant species. Thus, Rainier Mesa provided data on *Sceloporus occidentalis* and *Uta stansburiana* (Tanner and Hopkin 1972, Tanner 1972). Three study plots in Frenchman Flat examined *Crotaphytus wislizeni* (Tanner and Krogh 1974), *Phrynosoma platyrhinos* (Tanner and Krogh 1973), and *Callisaurus draconoides* (Tanner and Krogh 1975). Data from the Mercury Valley plot were included in some of the reports listed above.

In three of the five study plots, can pitfall traps were used; this enabled us to at least sample most of the species, particularly small lizards and snakes, that occurred in the habitat being studied. In the other two plots lizards were caught and marked by means of a noose.

At the Frenchman Flat Plot 2 (a rocky hill completely surrounded by desert flats and situated west of the Mercury highway and south of the Kane Springs road), small populations of *Crotaphytus collaris* and *Sauroradus obesus* were studied. At the Mercury Valley plot some data were obtained for *Coleonyx variegatus* and *Chionactis occipatalis.* Although only fragmentary data are presented, it does seemingly have merit.

Chionactis occipatalis talpina Klauber

We marked 62 individuals; of these 5 were recaptured once, and one twice. All recaptures were within 40 to 180 feet of the original capture, and 4 were recaptured two years after the original capture. Although these data do not substantiate a home range, they do indicate a relatively small "homing" area for this species. The can traps were set 40 feet apart in rows of 10 traps, and in rows numbered from A to T. Number 16, a young adult (S-V 225 mm), moved from G-8 (15 June 1966) to F-3 (5 August 1967) and to C-5 (5 June 1968).

The smallest individual marked was a hatchling marked 28 August 1969 with a S-V of 109 mm. The largest female was 291 mm S-V and the largest male was 287 mm. Individuals were considered adults if they were 250 or more in S-V length. Weight of adults varied with size and, in females, before eggs were layed. In adults, weights ranged from 6 to 10.4 grams.

Growth

Three of those recaptured were juveniles or subadults and show the following growth:

---

[1] Life Science Museum, Brigham Young University, Provo, Utah 84602.

No. 7 marked 15 August 1965 S-V 215 mm. Recaptured 5 June 1967 S-V 236 mm growth, 21 mm in 21½ months.

No. 12 marked 3 June 1966 S-V 239 mm. Recaptured 5 June 1968 S-V 251 mm growth, 12 mm in 24 months.

No. 16 marked 15 June 1966 S-V 225 mm. Recaptured 5 August 1967 S-V 250 mm. Recaptured 5 June 1968 S-V 251 mm growth, 25 mm in 13⅓ months.

Growth after individuals attain 250 mm in S-V length is seemingly slowed to a few mm per season, or, as in number 16, growth of no more than 1 mm in 24 months. Our data indicate that subadults may grow 0.5 to 2 mm per month, and show that from hatching to the largest adults they provide a S-V growth of approximately 180 mm. We do not have any data on longevity.

Coleonyx variegatus utahensis Klauber

At the Mercury Valley study plot we marked 115 individuals, and of these 33 were recaptured; 23 once, 7 twice, 2 three, and one five times. These data do not provide sufficient information to establish with certainty a home range size for this species. We conclude this in spite of the fact that many individuals were recaptured not far from their original capture, but only a few were recaptured more than twice. Those recaptured three or more times during two or more years do indicate a relatively small home range.

Females were gravid during July and early August in 1965. Hatchlings were seen in August. The earliest seen by us was 10 August 1966. Hatchlings during August (10th to 30th) from 1965–1969 range in size from 32 to 40 mm. It is assumed that the larger hatchlings seen in late August had been extant for several weeks, thus accounting for their larger size. Twelve juveniles caught in June (5th to 29th) ranged in size from 45 to 58 mm. Growth of hatchlings continues into September and begins again in April or early May; this accounts for the 10 to 15 mm of added growth seen in June.

Growth continues so that by August most juveniles have reached a S-V length of at least 60 mm, and by the next June are between 65 to 70 mm, most nearing 70 mm. The largest female individual seen measured 73 mm in S-V, was gravid, and weighed 6 grams on 1 August 1965.

Crotaphytus collaris bicinctores
Smith & Tanner
Great Basin Collared Lizard

Five adults were marked in 1965–1966 at the Frenchman Flat Plot 2. Each of these were recaptured or observed many times until the plot was closed in 1971. The habitat is a rocky ridge approximately 500 yards long and about half as wide. It rises to a peak in the middle and was used during the open air atomic testings as an observation point. On its top was a pole, which we refer to as the flag pole. Because of the openness of the habitat, the lizards moved over large areas within a loosely considered home range; this was quite in contrast to the limited space available to lizards in the study by Fitch (1956). Number 5 was observed during five years and traversed the southeastern side of the ridge, a linear distance of 680 feet. Although the others were not observed to travel this far, the home ranges, if indeed such occur, were large. There was an overlapping of ranges, even by males, a condition perhaps related to the openness of the large range and the small number of individuals present. We assumed the small population to be related to the food supply. We did not see many insects, and a population of *Sceloporus majester* shared the habitat and the food.

The lizards were easily spotted on rocks, usually on those higher than others nearby. They were not easily frightened, so we could observe them at close range. On 9 June 1966 we observed number 2, an adult male, vigorously active around a large rock near the flag pole (F-10). As we approached the rock, we noted a swarm of flying ants around the rock, and as the ants fluttered and tumbled over and down the rock, they were eaten by the lizard. At times he would feed on four to six ants in rapid succession, when they were available at the base of the rock. He would jump to capture flying ants if others were not available on the ground. He was relatively tame and paid little attention to us, even though we were only a few feet away.

On 1 July 1966, number 1, an adult female, was recaptured at G-6; on being released she moved up the ridge to F-10 and soon thereafter was observed eating flying ants that were still swarming on a rock near the flag pole.

The basking lizards were seen to leave their rock perch and chase a short distance, and then return. Number 5, an adult female, was observed on a rock near H-11 (about 100 feet from the flag pole); after observing for some time, we threw small rocks near her, and each time she responded by rushing to the spot where the rock lit. We were about 40 feet away, and by continuing to throw pebbles we were able to draw her right up to us. Each time after chasing a rock she would perch on a nearby rock and watch. Our observations of feeding activities compare similarly to those of Fitch (1956), and indicate a series of similar activity and feeding behaviors.

We did not see hatchings at this plot, although each of the females was observed to be gravid on 29 June 1966. Growth was observed in three, with numbers 2 and 3 (who were 103 and 89 mm in S-V length) showing no growth. Number 5 was 79 mm in S-V on 12 June 19667, and had grown to 95 mm on 15 May 1971. Weight during this same period increased from 21 to 28.8 grams; only gravid females weighed more (number 3 on 12 June 1966 weighed 33 grams).

Although we do not have data for complete growth and longevity, we do recognize this species as one with perhaps as long or longer life span than other lizards at this plot, except for *Sauromalus*. By comparing the size of number 5 (79 mm) to specimens in our preserved collection, we were not able to determine if she was nearing one or two years. Her size would represent only one year if based on data for the eastern subspecies (Fitch 1956). The study by Fitch shows rapid growth, with some individuals reaching full adult size in one year, an indication of abundant food and perhaps more favorable climatic conditions. The desert foothills and valleys of the Frenchman Flat area (Tanner and Hopkin 1972, Fig. 4) are dry and hot for most of June through September, with only an occasional thunderstorm. This not only affects the activities of the lizards, but also seemingly dries up the vegetation and may reduce the availability of insect food. In spite of the fact that the two studies are of two widely separated, distinct subspecies, we believe that environmental factors are extremely important in providing the differences in growth rate. When last seen, number 5 (15 May 1971) was in apparent good health and was either in her sixth or seventh year.

Cnemidophorus tigris tigris Baird & Girard
Great Basin Whiptail

Our field data concerning reproduction, growth, and longevity confirm previous studies such as those of Tanner and Jorgenson (1963), McCoy and Hoddenbach (1966), Burkholder and Walter (1973), and Turner, Medica, Lannom, and Hoddenbach (1969). The study by Tanner and Jorgenson (1963) suggested that aestivation, or early hibernation, occurs in early summer. We have observed this during a five-year study of populations at our study plots in Frenchman Flat and Mercury Valley. At both plots there was a noticeable reduction in the number of adults seen beginning in mid-July; the last adults were seen occasionally until mid-August. The latest record we have of an adult (92 mm S-V) was 26 August 1965. During August, hatchlings and second-year juveniles are seen, but by September only the year's hatchlings, ranging in size from 40 to 55 mm in S-V length, are seen. This does not mean that an occasional adult may not be seen, but our record indicates that a decided reduction in activity occurs each year beginning in mid-July. By far the greatest activity is in May and June.

We also noted that adult individuals marked in June or July, and then recaptured in April or May (soon after becoming active the next year), invariably had lost several grams of weight. Examples are toe-mark number 2-4, 8 June 1967, S-V 91, weight 24.8 grams; recaptured 7 April 1968, S-V 88, weight 20.8 grams. This individual was seen again on 4 May 1968 with a S-V of 93 and 23.1 grams. Number 1-6 marked 7 June 1966, S-V 99, weight 26 grams, recaptured 7 April 1968, S-V 96, weight 25 grams. Our data suggest that the early hibernation has the effect of reducing size and weight, which is rapidly regained by adults in June.

Sauromalus obesus obesus Baird
Western Chuckwalla

A population of chuckwallas were seen in Mercury Pass as we traveled from Mercury to our study plots in Frenchman Flat and Rainier Mesa. As time and opportunity was available, we marked 45 and recaptured 17; 9 once, 5 three, and 3 four times. No attempt was made to determine home range size, although our records indicate that certain rocks with suitable cracks and holes served as a home base around which they foraged and sunned.

As we continued to mark and recapture, we noted considerable growth in both size (mm) and weight (grams). Three males provided the following data: Number 2 on 30 June 1965 had S-V 175 mm and weighed 238 grams. On 29 June 1966 S-V 250 and weighed 315 grams. On 4 May 1968 only 2 mm of additional growth had occurred, but he had gained 80 additional grams to weigh 395 grams.

Number 4 on 16 July 1965 had a S-V of 150 and weighed 159 grams. On 28 May 1966 the S-V was 173 and weighed 210 grams. On 11 June 1968 he was S-V 185 and weighed 287 grams.

Number 6 on 21 July 1965 was S-V 154 and weighed 146 grams. On 28 June 1967 number 6 (two years' growth) was S-V 181 and weighed 251. This individual had averaged over 50 grams per year, but only 27 mm in S-V length.

We noted that the greatest growth of those marked occurred in the first three years; this is particularly true for the S-V length. After three years, most growth was in terms of added weight. Males were larger than females. The largest male (number 7) seen weighed 432 grams and was at least five years old. This individual gained only 39 grams in 3 years (393 grams on 28 May 1966 to 432 grams on 13 June 1968). Our data indicate that, after the S-V length of 200 mm is reached, a considerable slowing in length growth occurs; but, as noted above, increase in weight continues.

We noted courtships in May and early June, and that females were gravid in July. Three clutches of eggs were laid in July, and ranged in number from 4 to 14.

Literature Cited

Burkholder, G. L., and J. M. Walker. 1973. Habitat and reproduction of the desert whiptail lizard, *Cnemidophorus tigris* Baird and Girard at the northern part of its range. Herpetologica 29:76–83.

Fitch, H. S. 1956. An ecological study of the collared lizard (*Crotaphytus collaris*). Univ. of Kansas Publ. Mus. Nat. Hist. 8(3):213–274.

McCoy, C. J., and G. A. Hoddenbach. 1966. Geographic variation in ovarian cycles and clutch size in *Cnemidophorus tigris* (Teiidae). Science 154:1671–1672.

Tanner, W. W. 1972. Notes on the life history of *Uta s. stansburiana*. BYU Sci. Bull., Biol. Ser. 15(4):31–39.

Tanner, W. W., and J. M. Hopkin. 1972. Ecology of *Sceloporus occidentalis longipes* Baird on Rainier Mesa, Nevada Test Site, Nye County, Nevada. BYU Sci. Bull., Biol. Ser. 15(4):1–31.

Tanner, W. W., and C. J. Jorgenson. 1963. The application of the density probability function to determine the home ranges of *Uta stansburiana stansburiana* and *Cnemidophorus tigris tigris*. Herpetologica 19(2):105–115.

Tanner, W. W., and J. E. Krogh. 1973. Ecology and natural history of *Phrynosoma platyrhinos*, Nevada Test Site, Nye County, Nevada. Herpetologica 29(4):327–342.

———. 1974. Ecology of the leopard lizard, *Crotaphytus wislizeni* at the Nevada Test Site, Nye County, Nevada. Herpetologica 30(1):63–72.

———. 1975. Ecology of the zebra-tailed lizard *Callisaurus draconoides* at the Nevada Test Site. Herpetologica 31(3):302–316.

Turner, F. B., P. A. Medica, J. R. Lannom, and G. A. Hoddenbach. 1969. A demographic analysis of fenced populations of the whiptail lizard *Cnemidophorus tigris*, in southern Nevada. Southwest. Natur. 14:189–201.

NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE)

Stephen L. Wood[1]

ABSTRACT.— The following species of Scolytidae (Coleoptera) are described as new to science: *Amphicranus splendens, Araptus micropilosus* (Mexico), *Araptus morigerus* (Panama), *Araptus placetulus* (Mexico), *Chramesus bispinus* (Colombia), *Cnesinus aquihuai* (Mexico), *Cnesinus atrocis* (Panama), *Cnesinus meris* (Colombia), *Dendrocranulus gracilis, Hylastes retifer, Hylocurus prolatus, Micracis burgosi, Phloeotribus perniciosus, Pseudothysanoes fimbriatus, Pseudothysanoes pini, Scolytodes pilifer, Scolytus binodus* (Mexico).

While my taxonomic monograph of the Scolytidae of North and Central American (Wood 1982) was in press, several species new to science came to my attention. The following pages report 17 of these species in the genera *Amphicranus* (1), *Araptus* (3), *Chramesus* (1), *Cnesinus* (3), *Dendrocranulus* (1), *Hylastes* (1), *Hylocurus* (1), *Micracis* (1), *Phloeotribus* (1), *Pseudothysanoes* (2), *Scolytodes* (1), and *Scolytus* (1) from Mexico (13), Panama (2), and Colombia (2). Most of the Mexican material was received through Dr. T. H. Atkinson from the Colegio de Postgraduados, Institucion de Enseñanza y Investigaciones Agricolas, Chapingo, Mexico.

Amphicranus splendens, n. sp.

This species belongs to the *melanura* species group of the genus and is the most specialized known species in that group. It is distinguished from *argutus* Wood by the larger size, by the reticulate, dull frons, by the modified anterior margin of the pronotum, by the very different elytral declivity, and by other characters.

MALE.— Length 3.1 mm (paratypes: male 3.5 mm, female 3.0–3.2 mm), 3.2 times as long as wide; color very dark brown.

Frons broadly, uniformly convex; surface dull, very finely reticulate-granulate, punctures and vestiture virtually obsolete; a few setae at margins of eyes, epistomal margin ornamented by moderately abundant, long hair. Antennal club 1.7 times as long as wide, 1.7 times as long as scape; sutures 1 and 2 clearly indicated, slightly procurved; club densely covered by minute hair.

Pronotum 1.4 times as long as wide; sides straight and parallel on basal half, gradually tapering to angle on anterior margin; anterior margin straight on median half, formed by an elevated, continuous costa, meeting lateral margin at an abrupt, obtuse angle; summit indefinite, anterior to middle; low, almost scalelike asperities restricted to slightly less than anterior half; surface reticulate except for shining asperities and transverse rugae on more than posterior third; punctures minute, moderately close. Glabrous.

Elytra 1.8 times as long as wide, 1.3 times as long as pronotum; sides straight and parallel to base of declivital processes, posterior margin almost straight, feebly incised; disc shining, almost smooth, with rather numerous very feebly impressed lines, punctures minute, confused, rather close. Declivity subvertical; ventrolateral margin on more than lower third of a complete circle acutely, moderately explanate, entire at suture; upper margin not elevated at suture, interstriae 2 armed by a small, pointed tubercle borne on an obtuse elevation, summit of this elevation continuing to major process; major process occupying area of about interstriae 4 to 5, its lower margin at middle of declivity, its lateral surface continuing contour and sculpture of disc, its apex bluntly rounded, its free projection equal in length to width of antennal club, its mesal surface armed by a coarse, subapical denticle; face of declivity strongly, broadly concave, punctures fine, confused, obscure. Vestiture fine, short, obscure on declivital face, a few longer setae on lateral areas.

---

[1] Life Science Museum and Department of Zoology, Brigham Young University, Provo, Utah 84602.

FEMALE.— Similar to male except upper third of elytral declivity occupied by large, rounded protuberance in place of major process, small denticle at base on interstriae 2 present; antennal club without long setae on posterior face.

TYPE MATERIAL.— The male holotype, female allotype, and three paratypes were taken at San Rafael, Mexico, Mexico, 4-IX-1981, 2400 m, S-240, *Quercus*, T. H. Atkinson and A. Aquihua. The holotype, allotype, and paratypes are in my collection.

Araptus micropilosus, n. sp.

This species keys to *tenuis* (Blackman) in Wood (1982:933). It is distinguished by the very different female frons and by the strongly reticulate pronotum.

FEMALE.— Length 1.4 mm (paratypes 1.2–1.5 mm), 2.5 times as long as wide; color dark reddish brown.

Front flattened on a subcircular area occupying more than median three-fourths of area between eyes from epistoma to vertex, central half of flattened area micropunctate and ornamented by dense, minute micropile, surrounding area more coarsely punctured and bearing a rather sparse brush of long hair. Antennal club subcircular, without definite sutures (suture 1 apparently marked on some specimens).

Pronotum 1.05 times as long as wide; widest on basal fourth, tapered anteriorly, then rather narrowly rounded on finely serrate anterior margin. Summit indefinite, behind middle; posterior areas strongly reticulate, broad median line impunctate; remainder of disc with sparse minute punctures, these largely replaced by fine granules. Largely glabrous.

Elytra 1.6 times as long as wide; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed except 1 slightly, punctures small, shallow, in rows; interstriae about twice as wide as striae, smooth and shining except for rather abundant irregular lines, punctures absent. Declivity rather steep, convex; suture weakly elevated, striae 1 narrowly, rather deeply impressed, 2 as high as 1, and 1, 2, and 3 each with a row of very minute granules. Vestiture largely abraded on type, consisting of rows of erect, stout, blunt, interstrial bristles on declivity, each bristle about as long as distance between rows, spaced within a row by length of a bristle.

MALE.— Similar to female except frons convex coarsely, closely punctured, a feeble median carina on middle half, vestiture fine, sparse, inconspicuous.

TYPE MATERIAL.— The female holotype, male allotype, and seven paratypes were taken at Rancho Tepetates, Km 35 on the Veracruz–Xalapa highway, Veracruz, Mexico, 12-VI-1979, T. H. Atkinson. The holotype, allotype, and paratypes are in my collection.

Araptus blanditus Wood

Araptus blanditus Wood, 1974:47 (Holotype, female; Fortin de las Flores, Veracruz, Mexico; Wood Coll.)

In my collection three species have been confused under this name. The unique female type has the frons moderately concave, the pronotal disc is rather long, smooth, brightly shining, and without impressed points but with rather large, almost round, rather widely spaced punctures, the discal strial punctures are almost all in rows, declivital interstriae 2 is not wider than 1 and ascends rather conspicuously laterally, with the punctures of striae 2 comparatively coarse, and the antennal club is comparatively small and slender (1.5 times as long as wide). As pointed out below, slight but consistent differences separate this species from the two that follow.

Araptus morigerus, n. sp.

This species was incorrectly reported (Wood 1982:951) as *blanditus* Wood. It is distinguished from *blanditus* by the characters described below.

FEMALE.— Length 1.9 mm (paratypes 1.7–2.0 mm), 2.6 times as long as wide; color dark reddish brown.

Frons as in *blanditus*, except very slightly more strongly impressed, a small median tubercle on epistoma (obscure in a few specimens). Antennal club as in *blanditus*.

Pronotum as in *blanditus* except with moderately abundant impressed points, punctures smaller, closer, mostly elongate.

Elytra as in *blanditus* except strial punctures on anterior half of disc moderately confused, surface with moderately abundant impressed points; declivity shorter, steeper, punctures on striae 2 smaller, interstriae 2 wider, more nearly flattened; setae much finer.

MALE.— Similar to female except frons broadly convex, a feeble transverse impression just below middle, without any other impressions, punctures fine, rather abundant, vestiture fine, short, uniformly distributed; epistoma straight.

TYPE MATERIAL.— The female holotype, male allotype, and 33 paratypes were taken near Cerro Punta (labeled Volcán Chiriquí), Panama, 11-I-1964, 5500 ft, No. 376, broken branch, by me. The holotype, allotype, and paratypes are in my collection.

Araptus placetulus, n. sp.

This species is distinguished from *blanditus* Wood by the characters described below.

FEMALE.— Length 1.7 mm (males 1.9 mm), 2.4 times as long as wide; color very dark brown.

Frons similar to *blanditus* except less strongly impressed, surface more nearly granular, vestiture shorter (about two-thirds as long). Antennal club larger, stouter (1.3 times as long as wide).

Pronotum as in *blanditus* except anterior slope more gradual, disc slightly shorter, with numerous impressed points, punctures slightly smaller, much closer, elongate.

Elytra as in *placetus* on disc; declivity about as in *blanditus* except interstriae 2 more strongly impressed, almost flat, as wide as 1; vestiture fine as in *morigerus*.

MALE.— Similar to female except frons convex, a slight median callus at upper level of eyes, a transverse impression just below middle; epistoma slightly recurved, median third weakly elevated, slightly impressed in lateral areas before bases of mandibles, punctures very fine in central area on lower half, longer laterally and above.

TYPE MATERIAL.— The female holotype, male allotype, and one male paratype were taken at Uruapan, Michoacán, Mexico, 1-XI-1980, 1600 m, S-149, Aguacate, T. H. Atkinson and A. Equihua. The holotype, allotype, and paratype are in my collection.

Chramesus bispinus, n. sp.

This species is unique in the genus. It is distinguished by the bicolored pattern of scales and by the pair of large, hornlike spines on the elytral declivity.

MALE.— Length 1.8 mm (paratypes 1.9–2.2 mm), 1.9 times as long as wide; color a somewhat variable pattern of pale and dark scales.

Frons with a low, transverse elevation at level of antennal insertion, shallowly concave below this elevation, moderately concave above to upper level of eyes; surface subreticulate and finely punctured; vestiture of short stout setae, erect and slightly longer on lateral margins of upper area, epistoma with a brush of longer, yellow setae. Antennal scape with a tuft of long, yellow hair; club comparatively small for this genus, an apparent obscure surface indication of suture 1 present on anterior face.

Pronotum 0.77 times as long as wide; widest at base, sides moderately arcuate to rather broadly rounded anterior margin, a slight constriction just before anterior margin; surface smooth, shining, punctures small, close. Vestiture of short, abundant scales, those on basal third and lateral margins pale, dark in central and anterior areas; a few pale scales scattered in dark areas.

Elytra 1.3 times as long as wide, 1.8 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, punctures small, distinctly impressed; interstriae smooth, shining, about four times as wide as striae, lateral half of 1 to mesal half of 2 shallowly sulcate from base, broadening and deepening to become impression of declivity. Declivity commencing slightly behind middle, moderately steep; interstriae 1 distinctly elevated, strongly, rather broadly impressed from 1 to 3 on upper half, shallowly, more broadly impressed below; interstriae 3 armed slightly above middle by a pair of very coarse, hornlike spines directed caudomesad and slightly dorsad, each equal in length to width of antennal club. Vestiture of interstrial cover of short ground scales, each slightly longer than wide, and rows of erect bristles, those near base only slightly longer than ground scales, becoming longer and more slender posteriorly except on central part of lower declivity, these setae continue to apex of spines.

FEMALE.— Similar to male except frons less strongly impressed; tuft of hair on scape conspicuously smaller.

TYPE MATERIAL.— The male holotype, female allotype, and five paratypes were taken at Tenerife, Valle, Colombia, I-81 (three paratypes IX-80), tallos de curuba (passion flower vine stems, *Passiflora mollisima*), Patricia Chacon.

Cnesinus aquihuai, n. sp.

This species is distinguished from *atavus* Wood by the slightly larger, stouter body, and by the very different frons that is described below.

FEMALE.— Length 2.5 mm, 2.2 times as long as wide; color dark reddish brown.

Frons broadly, subconcavely impressed between lateral margins from epistoma to upper level of eyes; upper margin of impressed area at upper level of eyes abrupt, subcarinate; floor of impressed area reticulate, ornamented on a triangular area by special, compressed, reddish brown setae, base of triangle on epistoma, occupying median two-thirds, its apex on median line two-thirds distance toward upper level of eyes.

Pronotum and elytra essentially as in *atavus*.

MALE.— Similar to female except frontal impression somewhat irregular, ending gradually well below upper level of eyes; special ornamental setae absent, those present in lateral areas above epistomal area longer, yellowish.

TYPE MATERIAL.— The female holotype, male allotype, and two female paratypes were taken between Cuetzalan and Pasa del Jardin, Puebla, Mexico, 5-V-1981, 550 m, S-224, by T. H. Atkinson and A. Aquihua. The holotype, allotype, and paratypes are in my collection.

Cnesinus atrocis, n. sp.

This species is distinguished from the allied *bicolor* Eggers by the very different female epistomal callus and its setal ornamentation, by the more deeply impressed striae, by the larger strial punctures, and by the near absence of interstrial punctures except for those bearing the uniseriate rows of erect bristles.

FEMALE.— Length 2.3 mm, 2.7 times as long as wide; color reddish brown.

Frons as in *bicolor* except for epistomal callus; epistomal callus small, its upper margin forming a rather high, subacute, almost straight, transverse carina on more than median two-thirds, upper slope of callus (dorsad of crest of carina) ornamented by a single row of reddish, compressed specialized setae extending without interruption full length of carina.

Pronotum as in *bicolor* except punctures somewhat larger and more strigose, with limited confluence of strigosities on middle third.

Elytra about as in *bicolor* except striae more deeply, abruptly, narrowly impressed; bristle-bearing interstrial punctures almost uniseriate and distinctly crenulate, supplemental punctures obsolete, interstrial bristles coarser, rarely abraded.

TYPE MATERIAL.— The female holotype was taken near Cerro Punta (labeled Volcán Chiriquí), Panama, 11-I-1964, 5500 ft No. 388, from the twig of an unidentified sapling, by me. The holotype is in my collection.

Cnesinus meris, n. sp.

This species is distinguished from *bisulcatus* Schedl by differences in the epistomal callus and its setal ornamentation and in the sculpture of the pronotum.

FEMALE.— Length 2.4 mm, 2.6 times as long as wide; color dark reddish brown.

Frons as in *bisulcatus* except epistomal callus more abruptly elevated, its surface smooth, dull on large triangular area, upper margins of flattened area bearing one row of short, compressed, reddish brown ornamental bristles (in *bisulcatus* callus smaller, its margins less abrupt, upper two-thirds covered by ornamental setae).

Pronotum as in *bisulcatus* except punctures averaging smaller, not as close (very similar).

Male.— Similar to female except frontal callus greatly reduced, its ornamental setae finer, yellowish, more nearly normal.

Type material.— The female holotype, male allotype, and 12 paratypes were taken at La Cumbre, Valle, Colombia, 3-VI-1959, en café, by N. Muñoz. The holotype, allotype, and paratypes are in my collection.

Dendrocranulus gracilis, n. sp.

This species is distinguished from the allied *macilentus* (Blandford) by the much smaller size, by the larger pronotal and elytral punctures, by the very different female frons, and by other characters described below.

Female.— Length 1.4 mm (paratypes 1.3–1.6 mm), 3.2 times as long as wide; color black.

Frons broadly convex except flat on triangular area occupying median half at epistoma to obtuse apex well above upper level of eyes, this shining area minutely, rather densely punctured and ornamented by very fine, abundant, short hair, remaining area more coarsely punctured; vestiture less abundant.

Pronotum 1.2 times as long as wide; subquadrate, all margins moderately, about equally arcuate; surface obscurely subreticulate; indefinite summit near middle; discal area coarsely punctured, punctures largely replaced by slender elongate calluses in lateral areas; vestiture of sparse hair.

Elytra 2.0 times as long as wide, 1.7 times as long as pronotum; sides straight and parallel on basal three-fourths, very broadly rounded behind; striae not impressed, punctures rather coarse, in rows; interstriae as wide as striae, smooth, punctures uniseriate, half as large as those of striae. Declivity very steep, broadly convex, almost flat; surface sculpture as on disc; suture distinctly elevated, flat from striae 1 to 4, lower margin subacute to interstriae 4. Vestiture very fine, of rather short strial and conspicuous longer interstrial hair of moderate abundance.

Male.— Similar to female except frons more strongly convex above, a weak transverse impression at level of antennal insertion, coarsely punctured and sparsely pubescent over entire surface; declivital interstriae 2 rather broadly, moderately impressed, smooth, shining, impunctate.

Type material.— The female holotype, male allotype, and four paratypes were taken at Km 58 on the Xochimilco-Oaxtepec highway, Morelia, Mexico, 22-I-1980, 1970 m, S-19, Cucurbitaceae, T. H. Atkinson; six paratypes are from Uruapan, Michoacán, Mexico, 16-V-1981, *Sechium edulis*, A. Equihua. The holotype, allotype, and paratypes are in my collection.

Hylastes retifer, n. sp.

This species keys to *macer* LeConte in my monograph (Wood 1982:95), although its true affinities appear much closer to *mexicanus* Wood. It differs from all American species except *macer* by the uniformly reticulate pronotum and elytra. From *macer* it is distinguished by the stouter body, by the larger, stouter pronotum, with punctures much smaller and more abundant, and by the smaller, less strongly impressed strial punctures on the disc.

Male.— Length 5.4 mm, 2.8 times as long as wide; color black.

Frons essentially as in *macer* except more finely, closely punctured.

Pronotum 1.1 times as long as wide; sides parallel on basal half; surface uniformly, very finely reticulate (visible at minimum of 40X), punctures small, moderately deep, abundant, spaced by distances about equal to diameter of a puncture.

Elytra 1.9 times as long as wide; striae rather weakly impressed except near declivity, punctures rather small, moderately impressed; entire surface uniformly, finely reticulate; interstriae distinctly wider than striae, punctures fine, confused, rather abundant, 2 on posterior half of disc wider than 1 or 3 and weakly elevated; declivity as in *mexicanus* except reticulate.

Type material.— The male holotype was taken at Km 54 Carretera Toluca-Morelia, Est. de Mexico, 30-X-1980, 2520 m, *Pinus montezumae*, T. H. Atkinson and A. Equihua. The holotype is in my collection.

Hylocurus prolatus, n. sp.

This species is distinguished from *longipennis* Wood by the much weaker male frontal carina, by the less protuberant, more pubescent female frons, and by the sculpture at the basal margin of the declivity.

MALE.— Length 2.8 mm (paratypes 2.5–2.9 mm), 3.3 times as long as wide; color black.

Frons convex, a slight transverse protuberance on middle third, a weak transverse carina indicated about two-thirds distance from epistomal margin to upper level of eyes.

Pronotum and elytra as in *longipennis* except for basal area of elytral declivity; interstriae on posterior fourth of disc moderately convex, their summits interrupted at punctures (not clearly nodulate as in *longipennis*), their crests very briefly, longitudinally carinate at subabrupt margin of declivity (much more so than in *longipennis; declivital interstriae 9 more strongly elevated than in longipennis*, its crest much less strongly tuberculate.

FEMALE.— Similar to male except frons resembling female *longipennis*, with protuberance almost obsolete, median half of lower third impunctate, almost smooth, transverse area at upper level of eyes more finely punctured and ornamented by more abundant, fine, short, somewhat reddish setae; interstriae at base of declivity without longitudinal short carinae, margin less abrupt.

TYPE MATERIAL.— The male holotype, female allotype, and 18 paratypes were taken at Zacapoaxia, Puebla, Mexico, 6-V-1981, 2150 m, S-230, *Carya*, T. H. Atkinson and A. Equihua. The holotype, allotype, and paratypes are in my collection.

Micracis burgosi, n. sp.

The antennal scape of the female is the most remarkable found in any scolytid. Although the antennal club clearly places this species in *Micracis*, the protibia is more slender than seen elsewhere in this genus and the posterior face bears a few minute tubercles as in *Hylocurus*. Rather than suggest synonymy of these genera on the basis of this intermediate species, it is arbitrarily assigned to *Micracis* because of the antennal structure. It shares with *dimorphus* (Schedl) an identical protibia and antennal club, and a secondary shaft on the female scape, but it differs in numerous characters, some of which are described below.

FEMALE.— Length 2.6 mm (paratypes: male 2.2–2.4 mm, female 2.3–2.8 mm), 3.3 times as long as wide; color dark brown.

Frons feebly, transversely impressed at level of antennal insertion, flattened below, upper area to well above eyes weakly convex, central half smooth, brightly shining, impunctate; lateral and upper margins finely punctured and ornamented by moderately long, rather abundant setae. Antennal scape to insertion of funicle club shaped, its length equal to about one and one-half times width of eye, its dorsal margin ornamented by a fringe of rather abundant, long setae, most of these more than twice as long as this portion of scape, scape extended on dorsoapical angle above insertion of funicle into a long, slender shaft equal in length to combined length of funicle and club (or almost twice length of basal portion of scape), basal two-thirds of this shaft as wide as funicle, apical third twice this width, shaft glabrous except dorsal margin of its apical third ornamented by a tuft of very long setae, some of these setae longer than entire antenna; funicle and club as in *dimorphus*, except club very slightly more slender.

Pronotum 1.3 times as long as wide; outline as in *dimorphus*; posterior areas subreticulate, shining, crenulations continuing to base, except decreasing in size on posterior third and usually with rudimentary puncture on their posterior margins in this area.

Elytra 1.9 times as long as wide; sides straight and parallel on basal three-fourths, obtusely pointed behind; striae not impressed except 1 feebly, punctures moderately coarse, rather deep; interstriae one and one-half times as wide as striae, smooth, shining, punctures almost as large as those of striae, shallow, rather widely spaced. Declivity steep, convex; sculpture about as on disc except odd-numbered interstriae each with a row of about four fine tubercles, 9 moderately, subacutely elevated near its apex, crest of this elevation joining costal margin and continuing at descending height to sutural apex. Vestiture consisting of minute strial hair and rows of erect, coarse interstrial setae, those on disc about as long as distance between rows, almost twice as long on declivity.

Protibia about as in *dimorphus* except tubercles on posterior face smaller.

Male.— Similar to female except frons more strongly convex, coarsely punctured on upper two-thirds, vestiture simple, rather short, uniformly distributed; scape simple, without ornamentation.

Type material.— The female holotype, male allotype, and 25 paratypes were taken at Cuernavaca, Morelos, Mexico, 2-II-1981, *Delonix regia* bole, A. Burgos.

Phloeotribus perniciosus n. sp.

This species is distinguished from *destructor* Wood by the very different elytral declivity that superficially resembles some male *Hylocurus*.

Male.— Length 2.3 mm (paratypes 1.3–1.4 mm), 2.2 times as long as wide; color very dark brown.

Frons and pronotum about as in *destructor*, except pronotum less scabrous.

Elytra proportions and outline as in *destructor*; disc similar to *destructor* except interstrial crenulations lower, not as sharp, wider, mostly uniseriate, those on interstriae 1 to 9 near base of declivity largely subnodulate but ending at margin of declivity except 9 continuing as a strongly elevated, coarsely serrate, submarginal costa to apex; declivity about as steep but less strongly arched, with interstriae 1 to 8 unarmed, smooth, brightly shining, each with a uniseriate row of minute punctures; vestiture finer and longer than in *destructor*.

Female.— Similar to male except irregularly convex.

Type material.— The male holotype, female allotype, and three paratypes were taken along the Pátzucuaro-Ario de Rosales highway, Michoacán, Mexico, 31-X-1980, 2240 m, S-137, *Prunus serotina*, T. H. Atkinson and A. Aquihua.

Pseudothysanoes fimbriatus, n. sp.

This species is distinguished from *peniculus* Wood by the larger size, by the flat female frons, with shorter hair on the vertex, and by the different antenna.

Female.— Length 1.7 mm (paratypes 1.6–1.9 mm), 2.8 times as long as wide; color dark brown.

Frons flat below, very slightly convex above; smooth, shining, and impunctate on median area below, grading into reticulation upward and laterally then finally punctate-subgranulate; vestiture consisting of a fringe of long hair on upper margin, tips of longest extending slightly beyond middle of frons. Antenna similar to *peniculus* except segments of scape wider, club slightly narrower; scape, funicle, and club ornamented by rather abundant, long setae.

Pronotum and elytra as in *peniculus* except strial punctures on disc more distinct, interstrial punctures more nearly replaced by granules.

Male.— Similar to female except frons with a large, shallow, central fovea, reticulate in lower area, specialized setae on vertex absent, sparse setae uniformly distributed; antenna normal, setae sparse, rather short; pronotum and elytra as in male *peniculus* except declivital interstriae 3 with a row of rounded granules; elytral vestiture almost all abraded, apparently similar to male *peniculus*.

Type material.— The female holotype, male allotype, and 18 female paratypes were taken at Zacapoaxtla, Pueblo, Mexico, 6-V-1981, 2150 m, S-231, *Phoradendron*, T. H. Atkinson and A. Aquihua.

Pseudothysanoes pini, n. sp.

This species is distinguished from the closely allied *coniferae* (Wood) by the less strongly expanded female scape and by differences in the elytral declivity described below.

Female.— Length 1.6 mm (paratype 1.5 mm), 3.0 times as long as wide; color black, with white vestiture.

Head about as in *coniferae* except frontal setae less conspicuous; scape less strongly flattened, more nearly like male *coniferae* with larger tuft of hair.

Pronotum and elytral disc about as in *coniferae* except interstrial scales closer, shorter, and wider, each scale about as wide as long. Elytral declivity steeper and more broadly convex than in *coniferae*; interstriae 2 feebly impressed, 1 and 3 weakly convex on upper two-thirds, weak impression near apex extending from striae 1 to 4; interstriae 5 and 7 feebly elevated, joining, their continuing convexity forming ventrolateral margin and fusing with 1 at apex; scales on interstriae 1, 3, 5, and 7 forming double rows.

TYPE MATERIAL.— The female holotype and one slightly crushed female paratype were taken at Km 43 on the Texcoco-Calpualpan Highway, Mexico, Mexico, 17-III-1981, 2780 m, S-198, *Pinus hartwegii* x *P. montezumae*, T. H. Atkinson. The holotype and paratype are in my collection.

Scolytodes pilifer, n. sp.

This species is distinguished from *ingavorus* Wood by the much longer setae on the female frons, by the absence of reticulation on the pronotum, and by other characters described below.

FEMALE.— Length 1.4 mm (male 1.3–1.4 mm), 2.4 times as long as wide; mature color very dark brown.

Frons apparently as in *ingavorus* except setae on upper margin much longer, attaining epistoma (greater part of surface obscured by these setae).

Pronotum as in *ingavorus* except surfaces between asperities and between punctures smooth, brightly shining, punctures apparently slightly larger, deeper.

Elytra as in *ingavorus* except punctures deeper, strial and interstrial punctures subequal in size, those on declivity similar to disc, confused only on lower half, strial setae half as long, interstrial setae stouter.

MALE.— Similar to female except frons strongly convex, smooth, shining in central area, some reticulation elsewhere, a distinct transverse impression at level of antennal insertion, punctures rather fine, not close; vestiture of fine, short, sparse hair, interstrial bristles on declivity slightly stouter.

TYPE MATERIAL.— The female holotype,male allotype, and three paratypes were taken at Uxpanapa, Veracruz, Mexico, 26-V-1981, 120 m, S-287, A. Aquihua. The holotype, allotype, and paratypes are in my collection.

Scolytus binodus, n. sp.

Although this species bears a superficial rsemblance to *costellatus* Chapuis, it is not closely related. The unique feature is the presence of a widely separated pair of nodules on the female sternum 3. The male is unknown.

FEMALE.— Length 3.3 mm (paratypes 2.7–4.0 mm), 2.0 times as long as wide; color very dark brown to almost black.

Frons broadly convex; surface rather coarsely, convergently aciculate; a few fine punctures in grooves; vestiture of uniformly distributed fine long hair, upper margin on vertex bearing a row of coarser, longer hair, hair on lateral margins from epistoma to upper level of eyes longer, coarser, more abundant. Ventral half of suture 1 of antennal club with a septum, remainder of finely pubescent club unmarked by sutures.

Pronotum as long as wide; surface smooth, shining; median two-thirds very finely punctured, lateral areas more closely, somewhat coarsely punctured; glabrous.

Elytra 1.17 times as long as wide, 0.9 times as long as pronotum; surface smooth, shining; posterior third with striae and middle third of interstriae equally, rather deeply impressed (resembling *costellatus*), widths and depths of grooves equal on striae and interstriae, these grooves equal in width to convexities separating them from one another, strial and interstrial punctures in this area about equal; strial grooves continuing to base, interstrial grooves decrease in depth until almost obsolete at base, punctures decrease in size to half that of striae. A few short, stout interstrial setae on posterior half.

Anterior margin of sternum 2 costate, sternum 2 ascending at rate of about 80 degrees, smooth, shining, a few coarse punctures on its middle third; sternum 3 slightly longer than normal, impunctate, armed by a pair of moderately coarse, rounded tubercles, these dividing segment into approximately equal thirds; sterna 4 and 5 rather finely, closely punctured; a few hairlike setae on sternum 2.

TYPE MATERIAL.— The female holotype and 10 female paratypes were taken at Uxpanapa, Oaxaca, 24-V-1981, 120 m, S-182, *Combretom* sp., A. Equihua. The holotypes and paratypes are in my collection.

LITERATURE CITED

WOOD, S. L. 1974. New species of American bark beetles (Scolytidae: Coleoptera). BYU Sci. Bull., Biol. Ser. 19(1):1–65.

_____. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat. Mem. 6:1–1359.

TEMPERATURE-RELATED BEHAVIOR OF SOME MIGRANT BIRDS IN THE DESERT

George T. Austin[1] and J. Scott Miller[1]

Abstract.— Behavior of migrant birds in relation to temperature was studied and compared to that of resident species in the northern Mojave Desert. Migrants reduced foraging intensity above 30 C, but resident species showed no striking decrease in intensity of foraging at temperatures up to 35 C. Migrant species shifted activities to shaded microhabitats at temperatures between 20 and 30 C; the resident Verdin showed a similar shift at 35 C. Most migrants decreased the amount of time spent foraging at temperatures above 30; Verdins showed a similar but stronger response to temperatures about 30 C. Significant reductions in the use of hovering and hawking maneuvers were found among migrants at temperatures above 30 C. Migrants showed similar types of behavioral adjustments to temperatures as did resident desert species, but they responded earlier in the daily temperature cycle. Desert birds appear to correlate their daily activity strongly with temperature, but nondesert species may respond either to temperature or time of day.

Several studies have shown that resident desert birds react behaviorally to high ambient temperatures by shifting activity to cooler, shaded microhabitats and reducing the intensity and amount of activity (Smith 1967, Calder 1968, Ricklefs and Hainsworth 1968, Ohmart 1969, Austin 1976, 1978). Similar reductions in activity at high temperatures were found for certain nondesert species (Ricklefs 1971, Schartz and Zimmerman 1971, Verbeek 1972). It is unknown whether the midday depression in activity from a wide variety of temperature regimens is correlated with temperature or with time of day. Among certain desert species, this depression in activity is clearly a function of temperature (Ricklefs and Hainsworth 1968, Austin 1976).

Migrant birds in the desert, especially in fall, are exposed to temperatures that exceed considerably those encountered either on the breeding or wintering grounds. The potential lethality of desert heat and aridity was documented by Miller and Stebbins (1964). To migrate successfully through the desert may require physiological and behavioral adjustments by the species involved. Behavioral differences between migrant wood warblers (Parulidae) seen at cooler, higher elevations and those seen on the desert floor were noted previously by Austin (1970). This study was designed to detect and quantify behavioral changes over a range of temperatures by small passerine migrants during fall in the northern Mojave Desert.

Methods

Areas frequented by migrants were visited periodically throughout the peak migration period from 20 August to 25 September 1975. These included sites near Las Vegas, Tule Springs Park, Corn Creek Field Station of the Desert National Wildlife Range, and Moapa Valley, all in Clark Co., Nevada, and at Beaver Dam Wash, Mohave Co., Arizona. Most data on migrants were obtained at Tule Springs and Corn Creek, where numerous deciduous trees have been planted. Data on resident species and on a few migrants were obtained in natural desert riparian vegetation dominated by mesquite (*Prosopis juliflora*) near Las Vegas and at Corn Creek.

When a bird was encountered, the following data were recorded: species of bird; amount of time spent in each of several activities (sitting, preening, flying, foraging), timed with a stopwatch; amount of time spent in either shade or sun; number of perch changes per stopwatch-timed interval; number of each foraging maneuver (glean, hover, hawk as described by Root 1967); time of day and air shade temperature (T_a's noted on the half h). Several problems were encountered by the observer while following the individual bird under observation; the most notable of these was keeping track of the individual, which was often among several conspecifics. This situation, and the fact that migrants rarely remained in sight for long periods, resulted in most observations being of 3–5 minutes or less duration. Mean values and percentages were calculated using all periods of observation regardless of duration. Only observations greater than 1 minute in length were subjected to further statistical analysis.

---

[1] Nevada State Museum, Capitol Complex, Carson City, Nevada 89710.

Foraging maneuver data were treated with chi-square goodness of fit on the numerical data using Yates's correction where applicable. Feeding activity as perch changes per min and microhabitat usage expressed as proportion of time (transformed to arcsine; Zar 1974) spent in shade were analyzed using polynomial regression analysis. Diversity of foraging maneuvers and partitioning of time for T_a's above and below 30 C were calculated using the information-theoretical measure to the base e (H′). Differences between H′ at the two temperature ranges were tested using the methods outlined in Zar (1974). Statistical significance was set at $P \leq 0.05$ throughout.

Principal species studied were (minimum number of individuals observed are in parentheses): Warbling Vireo (*Vireo gilvus*) (20) and the warblers: Orange-crowned (*Vermivora celata*) (32), Nashville (*V. ruficapilla*) (25), Yellow (*Dendroica petechia*) (68), MacGillivray's (*Oporonis tolmiei*) (30), Wilson's (*Wilsonia pusilla*) (37), and American Redstart (*Setophaga ruticilla*) (7). Additional small samples (less than 50 minutes and 10 individuals) were obtained for other migrant and some resident species that will be mentioned in the text. Data were also obtained for the resident Verdin (*Auriparus flaviceps*); these were combined with data gathered for other studies (Austin 1976, 1978). Total sample for Verdins was approximately 30 individuals. Total amount of timed data for each temperature range is given in Table 1. Data collection was facilitated by the use of tape recorders. Observations were made on clear days under low wind conditions (< 8 km/h).

RESULTS

FORAGING RATE.— Rate of foraging by migrant species was comparatively rapid at T_a's below 30 C and sharply less rapid above 30 C (Table 2). On the average, foraging by migrant warblers was reduced by 10 perch changes per minute (37 percent) above 30 C. Greatest reductions were by Orange-crowned and Nashville warblers (43 and 47 percent). Analysis of these data by 2 C intervals indicated that 30 C was a well-defined point where foraging rate changed abruptly. Rate of foraging by Yellow Warblers, for example, average 22.1 and 15.2 perch changes per minute at 28–30 C and 30–32 C, respectively.

TABLE 1. Amount of observation time (seconds) obtained for foraging behavior.

	T_a (degrees C)				
	15–20	20–25	25–30	30–35	35–40
Verdin (V)[a]	10576	49475	45813	41179	59800[b]
Bewick's Wren (BW)	—	403	594	1235	—
Black-t. Gnatcatcher (BTG)	—	677	460	—	201
Warbling Vireo (WV)	1039	1732	1324	1283	—
Orange-cr. Warbler (OCW)	1883	1621	3583	2371	—
Nashville Warbler (NW)	1238	1409	1050	3357	1443
Virginia's Warbler (VW)	372	772	85	426	180
Lucy's Warbler (LW)	50	789	67	1023	—
Yellow Warbler (YW)	3179	5783	8307	16475	1327
Black-th. Gray Warbler (BTGW)	132	538	48	793	—
Townsend's Warbler (TW)	1966	—	344	698	—
MacGillivray's Warbler (MW)	2323	2928	1006	3181	681
Wilson's Warbler (WW)	2071	1341	4688	5259	370
American Redstart (AR)	657	533	801	593	—

[a] Species code in parentheses.

[b] T_a = 35–50 degrees C.

Apparently this response was more a function of T_a than time of day as indicated in Table 3. Rate of foraging during midday was greater on cool days than on hot days. Early morning foraging was at a somewhat reduced rate compared to later in the day at similar T_a's, accounting for the lower intensities at 15–20 C. Because of this, data for temperatures below 20 C were not used in regression analysis (below).

The slowly foraging Warbling Vireo showed only a slight decrease in foraging above 30 C. Its foraging rate, however, was lower than other species at all T_a's. Among migrant species with small samples, Virginia's Warbler (*Vermivora virginiae*) exhibited a gradual decrease in foraging with increasing T_a. American Redstart decreased foraging rate dramatically (by 44 percent) at 30 C and Townsend's Warbler (*Dendroica townsendi*) decreased foraging at about 25 C. The migrant Black-throated Gray Warbler (*D. nigrescens*) and the resident Bewick's Wren (*Thryomanes bewickii*), Black-tailed Gnatcatcher (*Polioptila melanura*), and Lucy's Warbler (*V. luciae*) apparently do not reduce foraging through at least 35 C. The Verdin exhibited a gradual decrease in rate of foraging with increasing T_a (Table 2; Austin 1976: Fig. 6); the most dramatic decrease (45 percent) was at 35 C.

Although the individual observations show considerable variability at all T_a's, foraging rates of the various species exhibit significant negative linear or quadratic relationships with T_a (Table 4). Although the variability involved is real on a short-term basis, we believe that the averages for each temperature range (Table 2) reflect a true and biologically important adjustment by these birds as T_a increases. Samples obtained over longer periods of time on an individual tend to show less variability, as indicated previously for the Verdin (Austin 1976).

MICROHABITAT USAGE.— Migrant species varied in the relative amount of time spent in shaded or exposed microhabitats (Fig. 1). MacGillivray's and Wilson's warblers foraged largely in the shade at all T_a's but especially at higher T_a's. In other transients, the proportion of time spent foraging in the shade was not as great at lower T_a's and increased rapidly with T_a. Warbling Vireos and Yellow Warblers made the most abrupt shift to shaded microhabitats at 30 C; Orange-crowned and Nashville warblers did so at 20 C. On the average, more than 95 percent of all foraging was in shade at T_a's above 30 C (Fig. 1).

The resident Verdin, in contrast, did not shift its foraging to predominately shaded microhabitats until T_a exceeded 35 C (Fig. 1; Austin 1976: Fig. 5). Above 35 C, about 15 percent of its foraging was still in vegetation exposed to the sun. Data for the Black-tailed Gnatcatcher indicated a similar pattern. Bewick's Wren and Lucy's Warbler appeared to forage predominately in the shade at all T_a's.

As with foraging rate, individual variability in microhabitat use (as proportion of time spent in shade) was great. Regression analysis of time spent in shade in relation to T_a indicated significant positive correlations for the six migrant species (Table 4). The variability and consequently low correlations for MacGillivray's and Wilson's warblers were likely due to the large number of relatively

TABLE 2. Mean number of perch changes per minute by birds in relation to ambient temperature.[a]

	Ambient temperature (degrees C)				
Species	15–20	20–25	25–30	30–35	35–40
Verdin	22.0	18.2	19.4	16.6	9.1
Warbling Vireo	15.4	16.4	14.8	11.2	–
Orange-crowned Warbler	21.6	26.2	23.0	13.1	–
Nashville Warbler	18.6	21.5	26.1	13.9	10.8
Yellow Warbler	22.4	22.4	23.2	13.5	13.4
MacGillivray's Warbler	20.6	26.7	21.2	15.1	–
Wilson's Warbler	32.7	37.0	34.6	26.6	19.8
American Redstart	31.6	41.1	39.5	23.3	–

[a] Observations summed for each temperature range regardless of duration of each observation; total observation time for each temperature range as indicated in Table 1.

short-duration (1–2 min) observations for these species. The statistically significant regressions, however, indicated that all six species increased the use of shade as T_a increased.

TIME BUDGET.— The partitioning of time by migrants varied with T_a. At lower T_a's, nearly all time was spent foraging and less than 5 percent spent sitting (Fig. 2). Above 30 C, the amount of time sitting increased to about 20 percent in most species. MacGillivray's Warbler did not increase time spent in inactivity above 20 percent until T_a reached 35 C. Wilson's Warbler did not sit more than 6 percent of the time at any T_a.

The Verdin increased sitting time gradually through 35 C. Above 35 C, the amount of time sitting increased sharply to 66 percent (Fig. 2; Austin 1978). The other three resident species did not increase time spent sitting above 30 C; too few data were obtained for T_a's above 35 C to draw conclusions.

FORAGING MANEUVERS.— At T_a's greater than 30 C, all migrant species decreased the use of hawking and hovering foraging maneuvers (Fig. 3). This change in foraging strategy above and below 30 C was statistically significant in all species except Black-throated Gray and MacGillivray's warblers

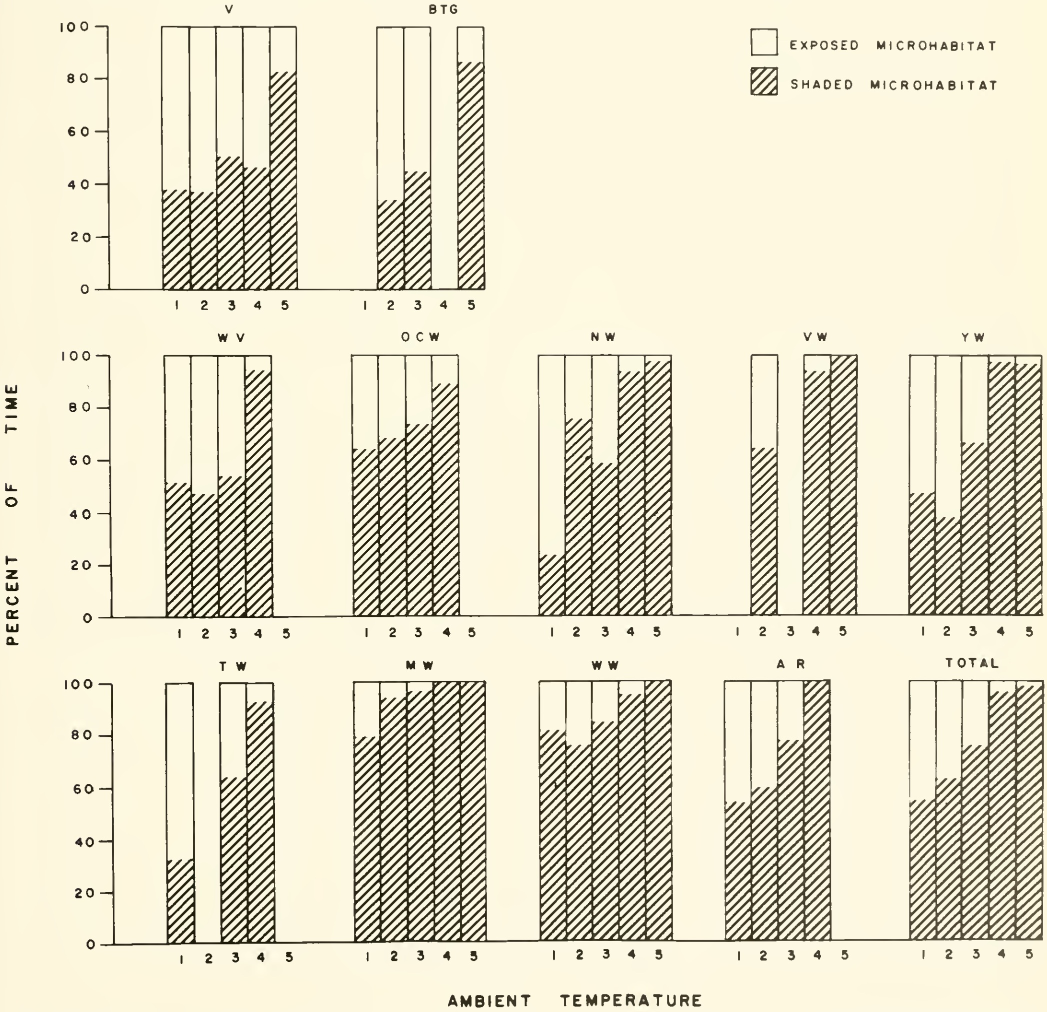


Fig. 1. Percent of time spent in shaded and exposed microhabitats as a function of ambient temperature by migrant and resident birds in southern Nevada. Temperature code is as follows: (1) 15–20 C, (2) 20–25 C, (3) 25–30 C, (4) 30–35 C, (5) 35–40 C. Species indicated by letters above bars are as coded in Table 1.

and was especially striking in Wilson's Warbler and American Redstart. Overall, both hawking and hovering were reduced proportionately, but Wilson's Warbler reduced hovering to a greater extent than hawking. When all three types of maneuvers were considered independently, Warbling Vireo, Yellow and Wilson's warblers, and American Redstart exhibited significant changes in overall foraging behavior. Larger samples for other species may show similar differences.

Samples for any one of the resident species were too small for analysis. The pooled data for the four species, however, showed no change in foraging strategy over the range of T_a's sampled.

DISCUSSION

Migrant species of birds showed behavioral changes at high temperatures that were similar in kind to those of resident species. Both reduced the amount and rate of foraging and shifted their activities to cooler microhabitats as ambient temperatures increased. Such changes in behavior reduce metabolic and environmental heat gain. In migrants the shift to cooler microhabitats tended to precede reduction in foraging rate, as was previously found for residents (Ricklefs and Hainsworth 1968, Austin 1976). This allows reduced heat stress but continued high rates of foraging. Changes in behavior were apparently more closely related to temperature than to time of day.

Although migrants were similar to resident desert species in the types of behavioral changes with increasing temperature, there were obvious differences in the temperature at which these occurred and the magnitude of change. Among resident species, foraging was reduced only at T_a's exceeding 35 C. Migrants generally decreased foraging rates at about 30 C. Similarly, there was an abrupt change in the partitioning of time by migrants at 30 C and by residents at 35 C. A shift to shaded microhabitats occurred in migrants at T_a's ranging between 20 and 30 C. Residents did not greatly increase the use of shade until T_a's exceeded 35 C.

At T_a's exceeding 35 C, the resident Verdin drastically reduced the amount of time spent foraging to less than 35 percent. No migrant species decreased foraging to less than 70 percent. This suggests that migrants may have to continue foraging at high T_a's to replenish energy stores and to maintain water balance, or that their adjustments to T_a are less refined than those of residents. The migrants' unfamiliarity with local conditions may also, in part, account for the increased foraging time. In any case, it seems likely that migrants need access to free water or an abundant food source during passage through the desert, which accounts for their relative rareness in the low desert away from riparian habitats.

Table 5 shows that diversity of foraging maneuvers decreased in all species at T_a's above 30 C; these differences were significant for all species except MacGillivray's Warbler. This decrease in diversity reflects the reduction of maneuvers involving flight (Fig. 3). Diversity in the partitioning of time increased significantly at T_a's above 30 C (Table 5). This reflected the increased amount of time spent resting at higher T_a's, whereas nearly all time was occupied by foraging at the lower T_a's (Fig. 2). Extreme weather conditions were shown by Grubb (1975) to affect foraging diversity of birds in eastern deciduous forest.

Diurnal rhythms in foraging behavior have long been recognized in birds (e.g., Palmgren 1949). It is generally recognized that there is a peak of activity in the morning that

TABLE 3. Foraging rate (number of perch changes per minute) as a function of T_a and time of day.

Species	Time / T_a	0600–1000 < 30 C	1000–1400 < 30 C	1000–1400 > 30 C	1400–1800 > 30 C
Orange-crowned Warbler		22.9	24.2	14.3	12.5
Nashville Warbler		19.4	23.1	14.0	12.8
Yellow Warbler		21.5	27.3	16.9	13.8
MacGillivray's Warbler		22.3	26.2	15.1	–
Wilson's Warbler		34.2	35.1	26.0	17.4

decreases toward midday and often increases again to another peak at the end of the day. In some species, this appears as a circadian rhythm, occurring at the same time of day under constant light conditions, as in the Arctic (Armstrong 1954) and under constant temperature conditions in the laboratory (Eyster 1954, Coutlee 1968, Smith et al. 1969). High temperatures modified this behavior in at least the White-crowned Sparrow (*Zonotrichia leucophrys*); activity at 33 C was 50 percent of that at 23 C. Daily activities of the House Sparrow (*Passer domesticus*) and Dark-eyed Junco (*Junco hyemalis*), however, were affected little at temperatures as high as 32 C and 35 C, respectively (Eyster 1954).

Field studies have demonstrated that a number of nondesert bird species reduce activity at high temperature. In the postbreeding Yellow-billed Magpie (*Pica nuttalli*), the amount of time spent foraging was negatively correlated with temperatures above approximately 25 C (Verbeek 1972). The male Dickcissel (*Spiza americana*) decreased various behaviors associated with reproduction and increased the amount of time spent resting as temperatures increased above 35 C (Schartz and Zimmerman 1971). Although total time spent foraging seemed unaffected, foraging intensity was reduced. The midday decrease in foraging time by the tropical Mangrove Swallow (*Iridoprocne albilinea*) was also suggested to be due to high radiational heat loading coupled with high humidity (Ricklefs 1971). Tropical flycatchers and Temperate zone swallows showed little or no reduction in midday activities (Ricklefs 1971).

Several desert species showed a close correlation between a reduced rate of activity or increased use of shaded microhabitats and increasing temperature (Dawson 1954, Smith 1967, Calder 1968, Ricklefs and Hainsworth 1968, Ohmart 1969, 1973, Austin 1976, 1978). Most species are highly active at midday in the cooler months of the year or on cool, cloudy days during midsummer. Behavioral changes observed in these studies may be actual adjustments in direct response to T_a, an indirect reflection of changes in distribution and activity of prey items or a combination of them. The available data suggest the latter. The Roadrunner (*Geococcys californianus*) maintained approximately constant rates of activity throughout the day in the laboratory at moderate temperatures (Kavanau and Ramos 1970). In the field, well-defined periods of inactivity in shaded areas were apparent during hot middays (Calder 1968, Ohmart 1973). Time of foraging was correlated with peak activity of their principal prey (Ohmart 1973). Captive Cactus Wrens (*Campylorhynchus brunneicapillus*) decreased activity and increased amount of time spent in shade with increasing T_a with food equally available under all conditions (Ricklefs and Hainsworth 1968). These changes in behavior were similar to those

Table 4. Regression analyses of the relationships between ambient temperature ($X = T_{a,b}$) and foraging intensity (Y = perch changes per min)[a] and proportion of time spent in shaded microhabitat (Y = arcsine of the proportion) by some migrant birds in the Mojave Desert.

Species	Dependent variable (Y)	Number of observations[c]	Correlation coefficient	Regression formula
Warbling Vireo	perch changes/min	25	0.477	$Y = 29.20 - 0.53X$
	% of time in shade[b]	21	0.558	$Y = -27.70 + 3.19X$
Orange-crowned Warbler	perch changes/min	33	0.695	$Y = 57.98 - 1.27X$
	% of time in shade[b]	35	0.652	$Y = -22.81 + 2.98X$
Nashville Warbler	perch changes/min	42	0.646	$Y = -155.97 + 13.01X - 0.24X^2$
	% of time in shade[b]	25	0.696	$Y = -6.45 + 2.71X$
Yellow Warbler	perch changes/min	100	0.500	$Y = 43.41 - 0.82X$
	% of time in shade[b]	81	0.661	$Y = 188.01 - 13.20X + 0.30X^2$
MacGillivray's Warbler	perch changes/min	36	0.514	$Y = 45.87 - 0.89X$
	% of time in shade[b]	33	0.351	$Y = 60.29 + 0.75X$
Wilson's Warbler	perch changes/min	71	0.467	$Y = 66.47 - 1.20X$
	% of time in shade[b]	41	0.442	$Y = 25.68 + 1.65X$

[a] Only data for ambient temperatures greater than 20 C were used, because foraging intensity was reduced in early morning at lower temperatures.

[b] Relationship expressed as arcsine Y = arcsine $a + bX$.

[c] Only observations > 1 min in length were used in regression analysis (see text).

observed in the field. Data on insects indicate that they reduce their activity and move into shaded microhabitats in response to increasing temperature (e.g., Clench 1966, Austin 1977).

Aside from differences in prey distribution and activity and temperature, other factors may account for some of the variability observed in behavioral modifications. The amount of time spent resting by the Dickcissel increased more rapidly at high T_a's when relative humidities were greater (Schartz and Zimmerman 1971). In the Las Vegas area during August and September, relative humidities average below 20 percent during daylight hours (Brown 1960) and are unlikely to be a major factor affecting behavior. Wind also affects bird behavior (Grubb 1975). In this study, however, observations were not made when the wind exceeded 8 km/h (most were taken on completely windless days), so wind is considered a constant.

Two distinct thermoregulatory problems arise when contending with desert heat; heat loading is often severe and, although low humidities promote effective evaporative cooling, water is largely unavailable. Species occurring in the desert are thus faced with opposing problems of water conservation and maintenance of heat balance. Such behavioral adjustments as shifting to shaded microhabitats and eventually reducing the intensity

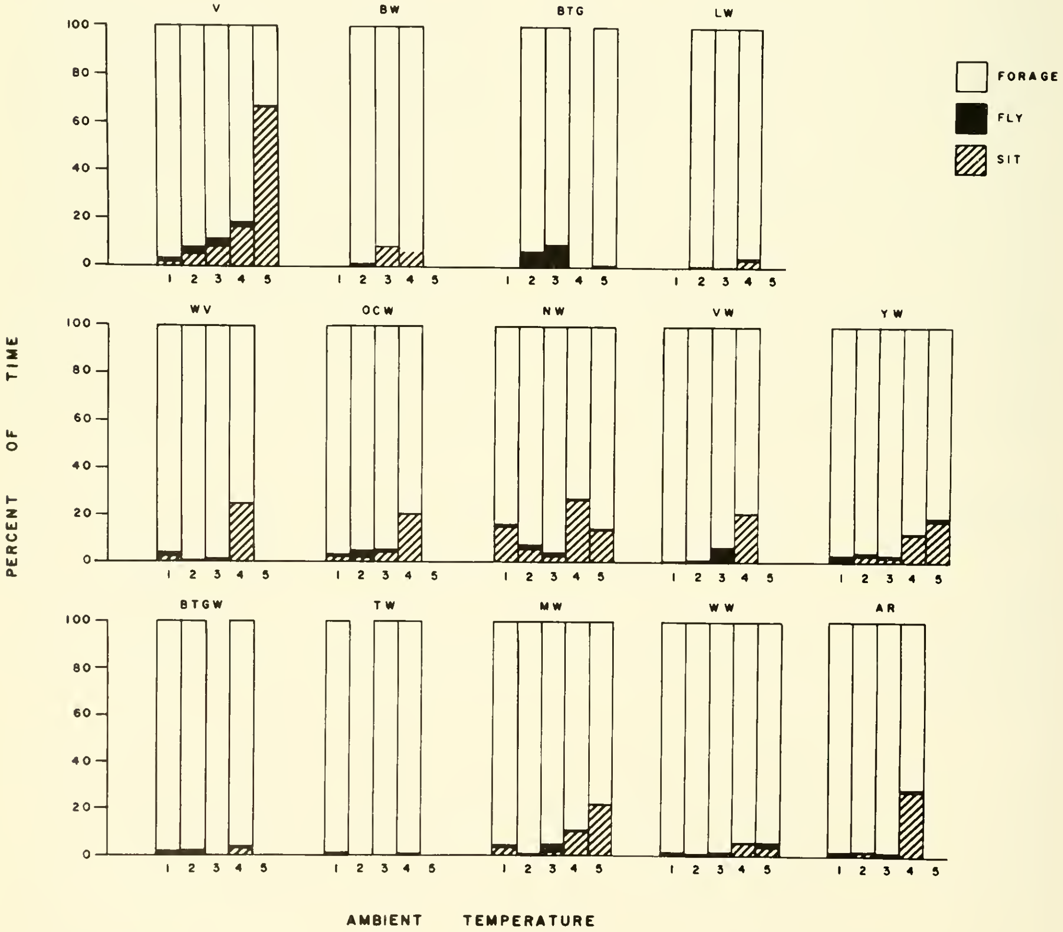


Fig. 2. Time budget of migrant and resident birds as a function of ambient temperature in southern Nevada. Temperature and species code as in Fig 1.

and amount of activity to a minimum may be a necessary and important means of contending with high temperatures. In non-arid localities behavioral means of reducing heat load may also be of some importance but for a different reason. Although temperatures tend to be lower than in arid areas, relative humidities are usually higher. This increased humidity reduces the effectiveness of evaporative cooling mechanisms due to a decrease in the vapor pressure gradient. Further studies of bird behavior under varying humidity conditions are highly desirable.

Acknowledgments

We thank W. G. Bradley, K. S. Moor, S. Naegle, R. D. Ohmart, R. E. Ricklefs, D. Thomas, and J. L. Zimmerman for suggestions on statistical procedures or comments and suggestions for improvements of the manuscript.

Literature Cited

Armstrong, E. A. 1954. The behavior of birds in continuous daylight. Ibis 96:1–30.

Austin, G. T. 1970. Migration of warblers in southern Nevada. Southwest. Natur. 15:231–237.

______. 1976. Behavioral adaptions of the Verdin to the desert. Auk 93:245–262.

______. 1977. Notes on the behavior of *Asterocampa leilia* (Nymphalidae) in southern Arizona. J. Lepid. Soc. 31:111–118.

______. 1978. Daily time budget of the post-nesting Verdin. Auk 95:247–251.

Brown, M. 1960. Climates of the states, Nevada. Climatography of the United States. U.S. Dept. of Commerce, Weather Bureau, No. 60-26.

Calder, W. A. 1968. The diurnal activity of the Roadrunner, *Geococcyx californianus*. Condor 70:84–85.

Clench, H. K. 1966. Behavioral thermoregulation in butterflies. Ecology 47:1021–1034.

Coutlee, E. L. 1968. Maintenance behavior of Lesser and Lawrence's goldfinches. Condor 70:378–384.

Dawson, W. R. 1954. Temperature regulation and water requirements of Brown and Albert towhees, *Pipilo fuscus* and *Pipilo aberti*. Univ. of California Publ. Zool. 59:81–124.

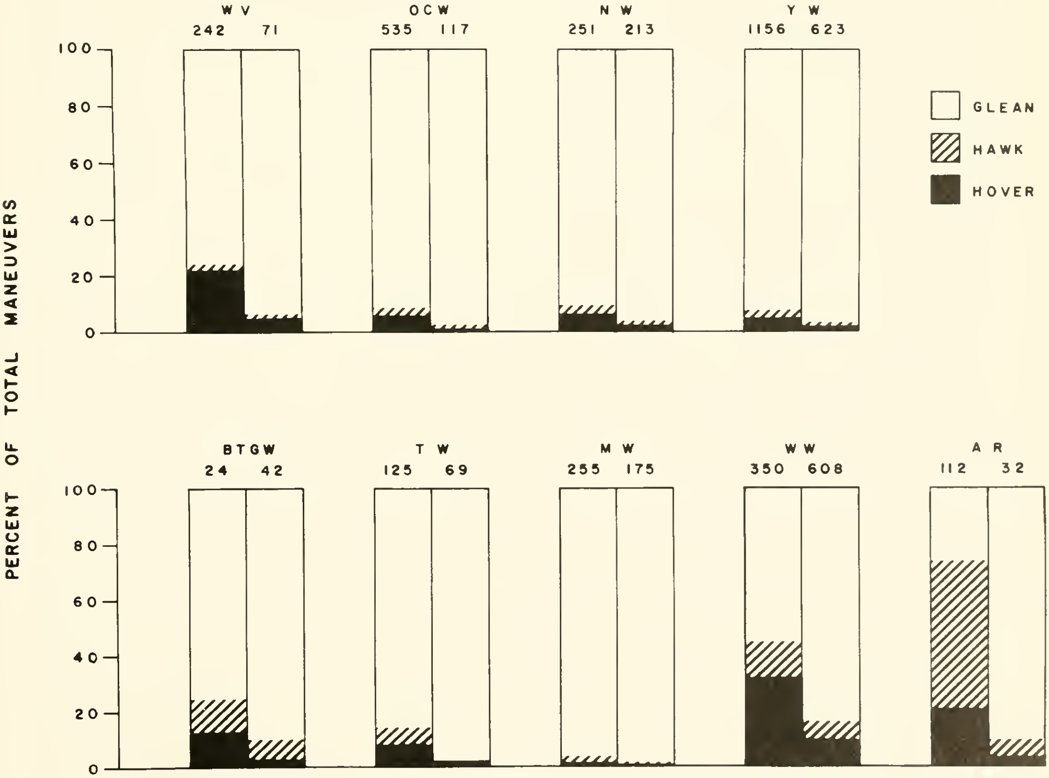


Fig. 3. Changes in the use of various foraging maneuvers as a function of ambient temperature by migrant birds in southern Nevada. Left-hand bar for each species represents temperatures less than 30 C; right-hand bar represents temperatures greater than 30 C. Species code as in Fig. 1. Number of foraging maneuvers observed indicated above each bar.

TABLE 5. Indices of foraging diversity (H′) by migrant birds in relation to temperature. Maximum diversity for 3 alternatives = 1.099 (to the base e).

	Time budget at T_a		Foraging maneuvers at T_a	
Species	< 30 C	> 30 C	< 30 C	> 30 C
Warbling Vireo	0.087	0.263	0.621	0.290
Orange-crowned Warbler	0.219	0.539	0.359	0.136
Nashville Warbler	0.340	0.584	0.376	0.185
Yellow Warbler	0.200	0.418	0.329	0.157
MacGillivray's Warbler	0.150	0.419	0.177	0.098[a]
Wilson's Warbler	0.080	0.256	0.961	0.567
American Redstart	0.112	0.661	0.949	0.371

[a] Difference not significant.

EYSTER, M. B. 1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds, Ecol. Monogr. 24:1–28.

GRUBB, T. C., JR. 1975. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. Condor 77:175–182.

KAVANAU, J. L., AND J. RAMOS. 1970. Roadrunners: activity of captive individuals. Science 169:140–147.

MILLER, A. H., AND R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. Los Angeles, Univ. of California Press.

OHMART, R. D. 1969. Physiological and ethological adaptations of the Rufous-winged Sparrow (*Aimophila carpalis*) to a desert environment. Unpublished dissertation. Univ. of Arizona.

———. 1973. Observations on the breeding adaptations of the Roadrunner. Condor 75:140–149.

PALMGREN, P. 1949. On the diurnal rhythm of activity and rest in birds. Ibis 91:561–576.

RICKLEFS, R. E. 1971. Foraging behavior of Mangrove Swallows at Barro Colorado Island. Auk 88:635–651.

RICKLEFS, R. E., AND R. R. HAINSWORTH. 1968. Temperature dependent behavior of the Cactus Wren. Ecology 49:227–233.

ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37:317–350.

SCHARTZ, R. L., AND J. L. ZIMMERMAN. 1971. The time and energy budget of the male Dickcissel (*Spiza americana*). Condor 73:65–76.

SMITH, E. L. 1967. Behavioral adaptations related to water retention in the Black-tailed Gnatcatcher (*Polioptila melanura*). Unpublished thesis. Univ. of Arizona.

SMITH, R. W., I. L. BROWN, AND L. R. MEWALDT. 1969. Annual activity patterns of caged non-migratory White-crowned Sparrows. Wilson Bull. 81:419–440.

VERBEEK, N. A. M. 1972. Daily and annual time budget of the Yellow-billed Magpie. Auk 89:567–582.

ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice-Hall, Inc.

DESCRIPTION OF A NEW *PHALACROPSYLLA* AND NOTES ON *P. ALLOS* (SIPHONAPTERA: HYSTRICHOPSYLLIDAE)

R. B. Eads[1] and E. G. Campos[1]

Abstract.— *Phalacropsylla morlani*, from New Mexico is described as new to science and figured. It is separable from the other species in the genus by the possession of 18 spines in the pronotal comb and by the distinctive shape and setation of the male distal arm of sternum IX. Other species in the genus have 14 to 16 spines in the pronotal comb. Host and distributional records for *P. allos* are given.

The description of *Phalacropsylla morlani* brings to six the number of known species in this montane genus. Other species are *P. paradisea* Rothschild 1915, *P. allos* Wagner 1936, *P. nivalis* Barrera & Traub 1967, *P. hamata* Tipton & Mendez 1968, and *P. oregonensis* Lewis & Maser 1978. Normal hosts of the *Phalacropsylla* are believed to be wood rats, *Neotoma* spp., and closely associated rodents and lagomorphs. A key is provided to aid in separating the species.

Phalacropsylla morlani, sp.n.
(Figs. 1–2)

Type material.— Holotype male ex *Ochotona princeps* (Richardson), Santa Fe, New Mexico, 10 Nov. 1958, H. B. Morlan, elevation ca 3048 m (10,000 ft). Morlan (pers. comm.) reports that a second male of this species with same collection data has been lost.

Diagnosis.— *Phalacropsylla morlani* most closely resembles *P. allos* and *P. nivalis* in that there are no long, curved spiniforms preapically on the outer surface of the male st IX, as is the case with *P. oregonensis*, *P. hamata*, and *P. paradisea*. In *P. nivalis* there is a deep sinus in the caudal margin of the male fixed process. In *P. allos* there is a shallow sinus in the caudal margin of the male fixed process, but the margin is merely sinuate in *P. morlani*. The pronotal comb of *P. morlani* has 18 teeth; there are 16 in *P. allos*.

Description of male.— *Head* (Fig. 1): Preantennal region with 2 slightly concave rows of bristles. Frontal row of 4 small, thin bristles with 3 fine intercalaries; ocular row of 4 much longer bristles; ca 5 thin bristles caudad of the ocular row. Maxilla narrow, acuminate distally extending to base of 4th segment of maxillary palpus; maxillary palpus extending almost to apex of coxa I. The 5-segmented labial palpus reaching beyond midportion of trochanter I. Postantennal region with bristles arranged 1-3-6 on one side, 2-3-6 on other, the caudal row with fine intercalaries; 16 or 17 fine hairs in an irregular row along the antennal fossa.

Thorax: Pronotum with a row of 7 large bristles separated by about same number of smaller ones per side; pronotal comb of 20 spines, all of approximately same length except for small ventralmost pair; second ventralmost pair appreciably wider than others. Mesonotum with a row of 6 large bristles and an equal number of fine intercalaries preceded by a row of 5 or 6 smaller ones and 15 to 20 short bristles scattered on cephalad margin; mesonotal flange with 3 pseudosetae per side. Mesepisternum with 2 subequal lateral bristles. Mesepimeron with 2 irregular rows of 2 bristles, caudal row of 6 or 7 long bristles with fine intercalaries, cephalad row of 5 or 6 smaller bristles. Metepisternum with a long bristle on subdorsal margin and a short one on the dorsal margin. Metepimeron with ca 5 lateral bristles arranged 2:2:1.

---

[1] Vector-Borne Viral Diseases Division, Center for Infectious Diseases, Centers for Disease Control, Public Health Service, U.S. Department of Health and Human Services, P.O. Box 2087, Fort Collins, Colorado 80522-2087.

Legs: Procoxa well provided with subequal bristles; dorsal ½ of anterior margin with row of short bristles; ventral ½ with 2 widely spaced long bristles, the ventral bristle reaching ca ½ length of profemur: subventral row of 6 long bristles extend well beyond trochanter. Profemur with row of short bristles on anterior margin, 2 submarginal bristles at distal third, and 2 irregular rows of ca 15 longer, thin, lateral bristles extending length of femur. Metacoxa outer surface without bristles on upper third, lower ⅔ with scattered bristles of unequal sizes, and an oblique row of 3 large bristles near ventral margin extending well below apex of trochanter; 3 large bristles near apex; inner surface of metacoxa with thin setae along anterior margin and submarginal, widening apically to include an oblique row of about 8 small spiniform bristles. Mesocoxa bristles on inner side limited to anterior margin with submarginal bristles on apical half becoming progressively larger toward apex; 3 large median bristles on ventral margin. Metatibia with 3 bristles, 2 long and 1 short at apex of dorsocaudal margin, the longest of which extends well beyond first tarsal segment; above these bristles are 6 notches bearing subequal, stout bristles, from apex to base 2:3:2:2:2:1.

Abdomen: Terga I–IV with apical spinelets: (1-0), (1-1), (1-1), and (1-0). Terga typically with a row of small bristles (1-5), followed by a row of larger bristles (4-7), alternating with smaller ones. Unmodified sterna with a vertical row of 1 to 3 bristles preceded by 1 or 2 smaller ones. Middle antepygidial bristle ca 2 × length of ventral bristle and almost 3 × length of dorsal bristle.

Modified abdominal segments: St VIII roughly triangular, higher than greatest width, devoid of bristles except for 1 large

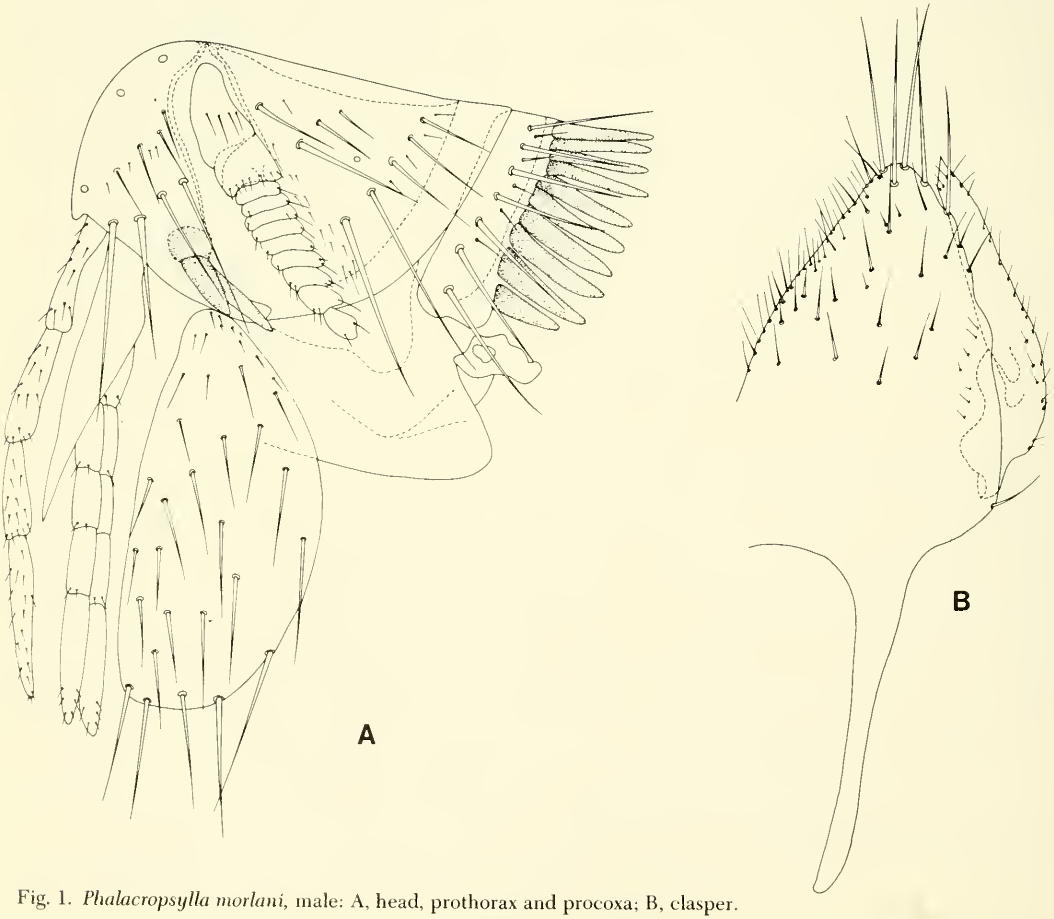


Fig. 1. *Phalacropsylla morlani*, male: A, head, prothorax and procoxa; B, clasper.

and 2 small bristles near midpoint of ventral margin; anterior margin fairly straight, evenly rounded at juncture with dorsal margin; dorsal and ventral margins join at blunt, evenly rounded, caudal apex. Immovable process large and well provided with bristles, especially on dorsal margin; caudal margin with 5 large bristles toward bluntly rounded juncture with dorsal margin; caudal margin sinuate but without pronounced sinus dividing process into lobes. Movable process of clasper ca 5 × as high as width at infrafoveal region, candle shaped, apex reaching almost as high as immovable process; anterior margin fairly straight, with a few scattered, marginal to submarginal setae; distal half of posterior margin fairly straight, basal half convex; thin bristles along most of the posterior margin, thickest on basal ⅔. Manubrum long and slender, about 20 × as long as broad at midpoint; anterior margin straight, posterior margin convex at midpoint.

St IX v-shaped, proximal arm much shorter than distal arm, and fish tailed at apex as with other species in the genus; distal arm ca 4 × as long as greatest width, a crescentic row of 8 subequal, spiniform setae toward apex, followed by a marginal row of thin bristles extending ca ¾ distance to base. Lightly sclerotized dorsal expansion of distal arm not discernible in holotype.

Discussion

Within the genus, *P. allos* has been recovered most frequently and from the widest geographical range. Described from specimens off *Neotoma cinerea*, Logan, Utah, it has subsequently been reported from California, Montana, New Mexico, and Wyoming. We have taken *allos* from March to August

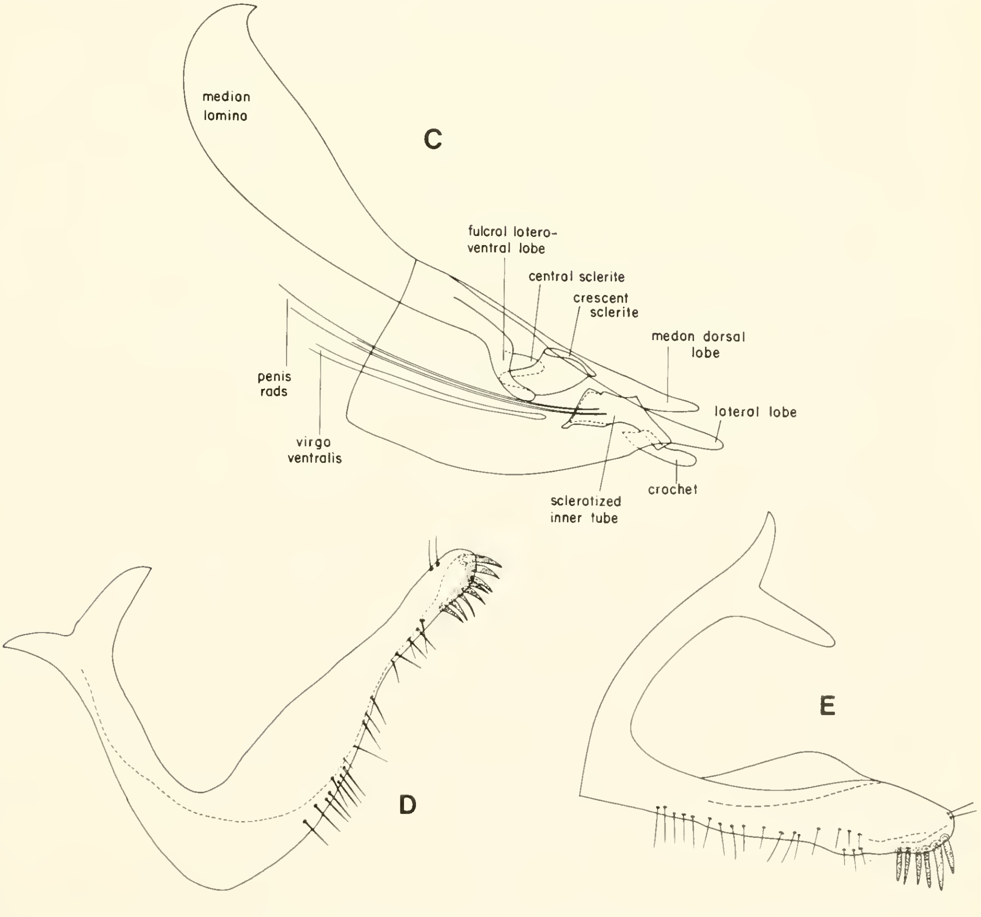


Fig. 2. *Phalacropsylla* spp., males: C, *morlani* aedeagus; D, *morlani* IX sternum; E, *allos* IX sternum.

in Larimer Co., Colorado, during year-round rodent trapping on the Weaver Ranch in 1977 as follows: 1 male ex *N. mexicana* 6 Aug.; 1 female ex *Reithrodontomys megalotis* 8 May; 1 male ex *Peromyscus difficilis* 5 March; 1 female ex *P. difficilis* 4 April; 1 male ex *P. difficilis* 8 May; 1 male ex *P. difficilis* 9 May; 1 female ex *Peromyscus maniculatus* 7 May; 1 male ex *P. maniculatus* 7 Aug.

The Weaver Ranch is 20 km N of Ft. Collins, Colorado, on U.S. 287. The relatively treeless, foothills habitat varies in elevation from ca 1600 m on the prairie to 1900 m at the highest point on the ridge, bisecting the ranch from north to south. The dominant shrub on the rocky slopes is mountain mahogany, *Cercocarpus montanus*.

Stark and Kinney (1969) have reported the recovery of 49 *P. allos* from California from 25 *N. cinerea* nests and 17 from 13 *N. cinerea* from shallow caves in the Lava Beds National Monument, Siskiyou Co. None were taken from 9 surface nests or 6 *N. cinerea* trapped on the surface. A single specimen was recovered from a *P. maniculatus* obtained at ground level. More recently, Dr. B. C. Nelson (pers. comm.) has collected *allos* in numbers from *N. cinerea* nests in the same caves: 21 males, 15 females, 9 Dec. 1976; and 1 male, 31 Jan. 1980.

Key to the species of *Phalacropsylla*
(Female of *morlani* unknown)

1.	Male	2
—	Female	7
2.	Fixed process of clasper divided caudally by a deep sinus	3
—	Fixed process of clasper without pronounced sinus, posterior margin sinuate	4
3.	Two long, curved spiniforms present preapically on inner surface of distal arm of st IX	*hamata*
—	No long, curved spiniforms on inner surface of distal arm of st IX	*nivalis*
4.	Long, curved spiniforms present preapically on inner surface of distal arm of st IX	5
—	Without long, curved spiniforms preapically on inner surface of distal arm of st IX	6
5.	Apex of movable process extending about to apex of fixed process	*paradisea*
—	Apex of movable process extending less than ⅔ height of fixed process	*oregonensis*
6.	16 teeth in pronotal comb	*allos*
—	20 teeth in pronotal comb	*morlani*
7.	Caudal lobe of st VII longer than broad	8
—	Caudal lobe of st VII broader than long	9
8.	Caudal lobe of st VII ca 1.5 × as long as broad	*nivalis*
—	Caudal lobe of st VII ca 1.9 × as long as broad	*allos*
9.	Caudal lobe of st VII 3.5 × as broad as long	*hamata*
—	Caudal lobe of st VII less than 2 × as broad as long	10
10.	Caudal lobe of st VII rectangular, broadly rounded at apex	*paradisea*
—	Caudal lobe of st VII more triangular, apex bluntly pointed and deflected ventrally	*oregonensis*

Acknowledgments

This species is named for the collector, Harvey B. Morlan, sanitarian director, USPHS (Ret.), who has contributed greatly to our knowledge of vector-borne diseases. Gary O. Maupin, VBVDD, and W. S. Archibald, formerly of VBVDD, were involved in the

collection of the *P. allos* in Larimer Co., Colorado. Dr. R. E. Lewis, Iowa State University, was consulted concerning the taxonomic status of *P. morlani.*

LITERATURE CITED

BARRERA, A., AND R. TRAUB. 1967. *Phalacropsylla nivalis,* a new species of flea from Mexico (Siphonaptera: Hystrichopsyllidae). An. Esc. Nac. Cienc. Biol. Mexico City 14: 35–46.

LEWIS, R. E., AND C. MASER. 1978. *Phalacropsylla oregonensis* sp. n., with a key to the species of *Phalacropsylla* Rothschild 1915 (Siphonaptera: Hystrichopsyllidae). J. Parasit. 64(1): 147–150.

ROTHSCHILD, N. C. 1915. On *Neopsylla* and some allied genera of Siphonaptera. Ectoparasites I: 30–44.

STARK, H. E., AND A. R. KINNEY. 1969. Abundance of rodents and fleas as related to plague in Lava Beds National Monument, California. J. Med. Ent. 6(3): 287–294.

TIPTON, V. J., AND E. MENDEZ. 1968. New species of fleas (Siphonaptera) from Cero Potosi, Mexico, with notes on ecology and host parasite relationships. Pacific Insects 10(1): 177–214.

WAGNER, J. 1936. Neue Nordamerikanische Floharten. Z. Parasitenkd. 8: 654–658.

VEGETATION OF THE MIMA MOUNDS OF KALSOW PRAIRIE, IOWA

Jack D. Brotherson[1]

Abstract.— One hundred and twenty-eight mima mounds were studied relative to their vegetational relationships in a tall grass prairie area of central Iowa. Mound origins are thought to be due to several phenomena but are most likely initiated and maintained by the activity of pocket gophers. Seventy-five percent of the plant species common to the mounds are prairie species. When vegetative composition of the mounds was compared to the adjacent prairie vegetation, however, they were only 35 percent similar. The mounds were shown to alter the original structure and composition of the prairie vegetation. The mounds, once formed, created a new microenvironment. Many species were shown to respond to this new habitat. The factors deemed most influential in affecting the vegetational changes were disturbance and microrelief. Study observations indicate that the mounds represent microsuccession sites and cause changes in prairie vegetation to earlier stages in the sere.

Provision for state-owned prairies in Iowa was made in 1933 when the State Conservation Commission prepared a report known as the Iowa Twenty-five Year Conservation Plan. In a section of that report the following proposal was recommended:

> Prairie Preserve—Recommended. Along the railroad rights-of-way, and here and there in small patches throughout the state, unbroken virgin prairie sod is still to be found. Some of these will be saved because they lie within protected areas, or simply because the ground cannot be used for farm purposes. But somewhere in Iowa a large enough original tract of prairie vegetation should be secured in order to save, under control of the state, the characteristic landscape, wild flowers, and wild life of the native prairies. Several tracts ranging from forty to three hundred acres have been found by the survey. The Conservation Plan includes a Prairie Preserve which will be one of the remaining original areas, or which may be produced by purchase of semiwaste land and bringing it back to prairie condition in a few years' time. (Hayden 1945)

Prairies now owned by the state of Iowa were purchased and set aside as natural areas with the intent that features typical of prairie landscapes, such as wild flowers and wildlife native to the tall-grass prairie region, could be preserved for posterity. It was also intended that these areas would be useful as game and wildlife sanctuaries; as examples of the native prairie soil types, where comparisons could be made with cultivated soils of the same soil association; and as reserves of prairie where scientific investigations could be made on problems concerning the native vegetations, floras, and faunas of the various topographic, climatic, and prairie districts throughout Iowa. Therefore, they were meant to serve as a reference point by which future generations could compare the influence of man on Iowa since settlement (Hayden 1946, Moyer 1953, Aikman 1959, Landers 1966).

Kalsow Prairie, 65 ha (160 acres) of unplowed grassland in Pocahontas County, Iowa, was purchased for these reasons in 1949. Since its purchase in 1949, it has been the object of studies on its vegetation, soils, management, insects, response to fire, mammals, and nematodes (Moyer 1953, Ehrenreich 1957, Esau 1968, Richards 1969, Brennan 1969, Norton and Ponchillia 1968, Schmitt 1969, Brotherson and Landers 1976, Brotherson 1980).

The characteristics of Iowa prairie in terms of vegetation types, structure, and general ecology of the dominant species was the subject of several papers during the 1930s and 1940s (Steiger 1930, Rydberg 1931, Weaver and Fitzpatrick 1934, Hayden 1943). These authors recognized the existence of six major types of grassland or vegetative communities and generally concluded that water relations, as affected by climate, soil, and topography, are responsible for local variations in the structure and distribution of prairie vegetation.

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Moyer (1953), Aikman and Thorne (1956), Ehrenreich (1957), Kennedy (1969), and Brotherson (1969) in more recent studies present ecological and taxonomic descriptions of four state-owned native prairie tracts. The vegetation complex as treated in these studies is limited basically to upland prairie. The studies also include information on soils, microclimate, topography, and management.

Investigations involving the distribution of individual species within the prairie association began with the work of Shimek (1911, 1915, 1925). Weaver (1930) and Weaver and Fitzpatrick (1932) discuss the role of the major grasses and forbs within the community. Steiger (1930) and Cain and Evans (1952) mapped the spatial distributions of several species. They conclude that the principal factors affecting the local distribution patterns of prairie species are as follows: (1) microclimatic conditions, (2) edaphic variations, (3) the biology of the species concerned, particularly methods of reproduction and dispersal, (4) the relations of the species and other organisms, animal as well as plant, occurring in the community, and (5) the element of chance in the dispersal and establishment of new individuals. Local distribution patterns of species have been of interest to many ecologists.

One factor influencing such distribution patterns in prairies across North America are mima mounds (Collins 1975, Del Moral 1976, and Mielke 1977). Such mounds, originally thought to be Indian burial mounds (Davids 1967), have been known to exist for many years. Their origin has frequently been contested in scientific literature. They have been considered the result of fossorial mammal activity, hydrostatic pressure, wind deposition, or several ground-frost phenomena (Scheffer 1947, Thorp 1949, Tester and Marshall 1961, Hansen 1962, and Davids 1967). Scheffer (1958), McGinnies (1960) and Ross et al. (1968), in reviews of mound development, indicate that none of the hypotheses concerning their origin is universally accepted. Ross et al. (1968) indicate that this disagreement is probably due to the description of different causes or combinations of causes at different locations.

This study was undertaken to provide information on the phytosociology of this particular prairie phenomenon. It includes information on species composition and distribution of the mounds and on the mounds' relationship to the prairie vegetation.

METHODS

This study was begun in the spring of 1967 and continued through the following year (1968) and into the summer of 1969. The study site (Kalsow Prairie) is one of four state-owned Iowa prairies. It is five miles northwest of Manson, Iowa, and comprises the NE ¼ of Section 36, Belleville Township, T 90 N, R 32 W, Pocahontas County. It occurs in a part of north central Iowa that was glaciated during the most recent advances of the Wisconsin Glacier and within the Clarion-Nicollet-Webster soil association area (Ruhe 1969). The area was chosen for study on the basis of its vegetational composition (i.e., floristic richness and the presence of several plant community types) and the presence of mima mounds found scattered across the 65 ha of the study area.

The vegetation of mima mounds was analyzed using two separate approaches. The first involved the identification and listing of all species found within their boundaries. The second utilized random plots to determine percent cover, composition, and interspecific relationships of species within these subcommunities.

Voucher specimens were collected in duplicate throughout the growing seasons of 1967 and 1968. All specimens were identified and identical sets have been deposited in the herbaria of Iowa State University, Ames, Iowa, and Brigham Young University, Provo, Utah. Nomenclature follows Pohl (1966) for the grasses, Gilly (1946) for the sedges, and Gleason (1952) for the forbs.

Quadrat Analysis

The vegetation of each mound was sampled by using a 20 × 50 cm (1000 cm²) quadrat (Fig. 3). The quadrats were located on a restricted basis to reduce bias and to keep adjacent quadrats at fairly equal distances apart. Sampling was done between 1 August and 15 September each year when most species had reached their maximum growth. Cover estimates were made for each quadrat through use of Daubenmire's (1959) method.

Coverage was determined separately for all species overlapping the plot regardless of where the individuals were rooted. Coverage was projected to include the perimeter of overlap of each species regardless of superimposed canopies of other species. The canopies of different species are commonly interlaced or superimposed over the same area; therefore, coverage percents often total greater than 100 percent.

The mounds were first located (Fig. 1) and permanently identified by a numbered stake placed at the west edge of the mound. Every

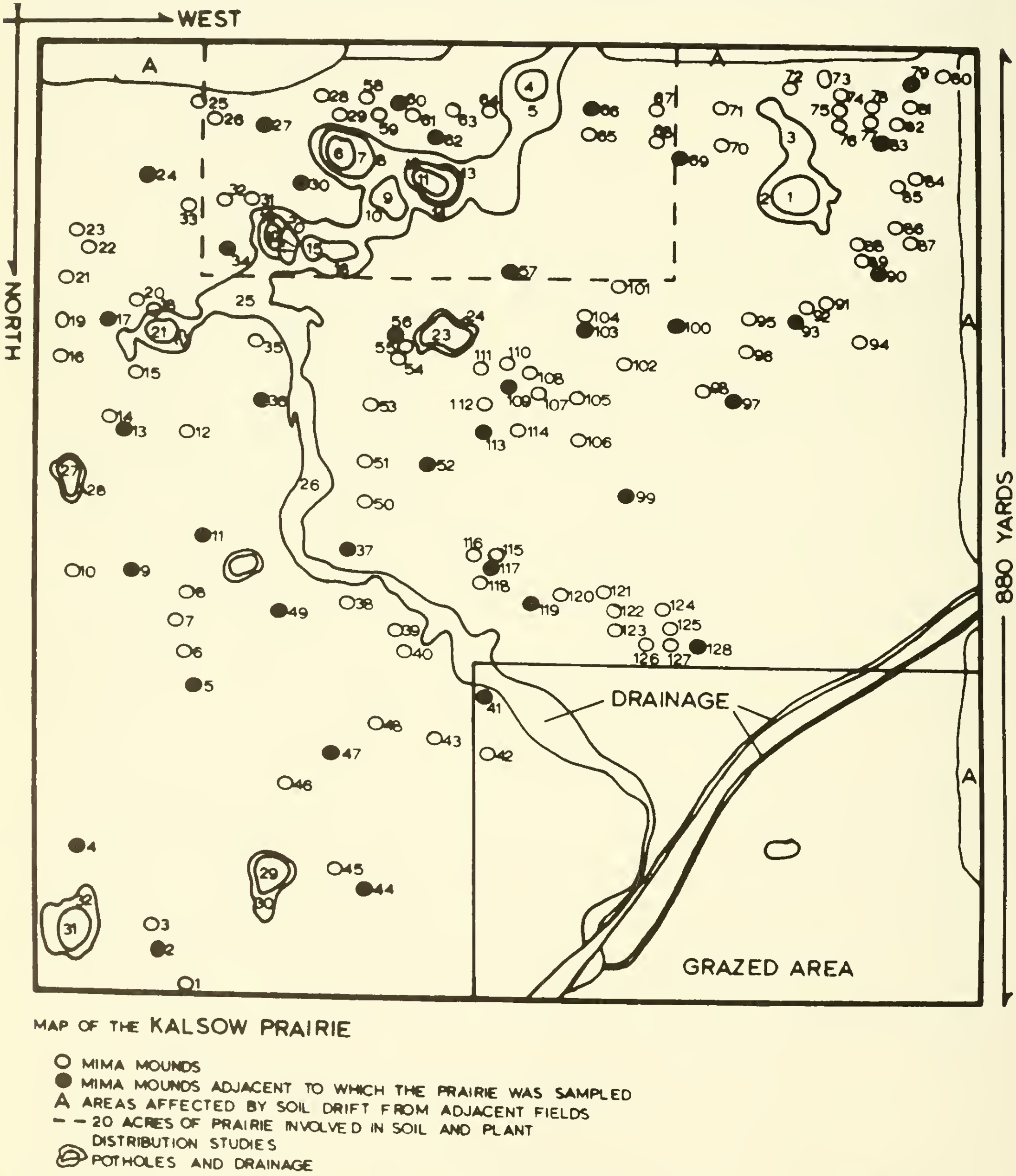

WEST
NORTH
880 YARDS
A
DRAINAGE
GRAZED AREA
MAP OF THE KALSOW PRAIRIE
○ MIMA MOUNDS
● MIMA MOUNDS ADJACENT TO WHICH THE PRAIRIE WAS SAMPLED
A AREAS AFFECTED BY SOIL DRIFT FROM ADJACENT FIELDS
– – 20 ACRES OF PRAIRIE INVOLVED IN SOIL AND PLANT DISTRIBUTION STUDIES
POTHOLES AND DRAINAGE

Fig. 1. Map of Kalsow Prairie showing the distribution of mima mounds.

mound was then sampled starting at the northeast corner of the mound and gridding the mound with quadrats placed every three steps. The number of samples varied with the size of the mound, ranging from 5 on the smallest to 45 on the largest. A total of 1549 samples was taken on 128 mounds. Mound dimensions were taken in north-south and east-west directions, and areas (in square feet) were obtained through the use of the ellipse area formula

$$A = pab$$

A is the area; $p = 3.1417$; a is the length; and b is the width of the mound.

Data was also taken to describe the prairie community adjacent to the mounds. This involved 444 samples taken adjacent to 37 selected mima mounds. Each mound was bisected by two transects oriented in north-south and east-west directions. Quadrats were then taken along these transects (Fig. 2) starting at the mound edge and progressing into the adjacent prairie. A total of 12 quadrats was taken adjacent to each mound, 3 in each direction. The quadrats were placed at 12-foot intervals.

Data Analysis

Data collected from quadrat studies, mapping studies, and topographic studies were used to describe generally the vegetation of the mounds. Frequency values and average cover values were determined for all species in every stand. Frequency values were determined by use of the following formula:

$$\text{Frequency (\%)} = \frac{\text{Number of plots of occurrence}}{\text{Total number of plots sampled}} \times 100$$

Cover values were determined by summing the midpoints of the cover-class ranges and dividing by the number of sample quadrats in the stand.

An ordination technique proposed by Orloci (1966) was employed to ordinate vegetation units within the different subcommunities listed above. Raw data were first summarized by hand calculation and then transferred to punch cards. This technique was completed on an IBM S360 Mod 65 computer. Through this technique the entities to be ordinated (i.e., plant species or stands of vegetation) are projected as points into n-dimensional space. Such points are positioned by attribute scores through the application of the R- and Q-techniques of factor analysis. Once established, this multidimensional array of points is then reduced to a three-dimensional system. This is accomplished by selecting the two most different stands or species and placing one at zero and the other at some distance along the abscissa. All other stands or species under consideration are then positioned linearly in relationship to these two extremes. This action thus establishes the X-axis. The above process is repeated until all points have been established in three dimensional space (i.e., Y and Z axes have been added). Coordinate values for the X, Y, and Z axes are given as output from the computer.

Expressions of interspecific association were attempted utilizing Cole's Index (1949). Step one in the computation of the index involves the accumulation of 2 × 2 contingency tables. Actual calculation of the index involves the formulas discussed by Brotherson (1980). Tests of statistical significance were performed by means of the Chi-square test. In all cases a single degree of freedom was used. Chi-square values greater than 3.84 were considered to be significant at the 5 percent level, and values greater than 6.63 were considered to be significant at the 1 percent level.

Graphic representation of data obtained from topographic studies and from ordination analysis was drawn by the computer.

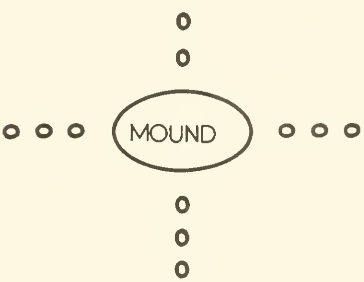


Fig. 2. Location of plots in upland prairie adjacent to selected mima mounds.

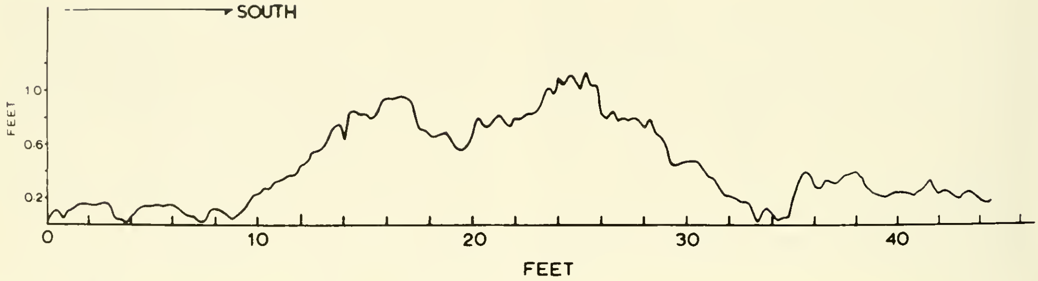


Fig. 3. Microrelief, determined in July 1968, of Mound 14 (Fig. 1), a typical mima mound, Kalsow Prairie.

Results

Historical information as well as evidence obtained in this study indicates that much of the Kalsow Prairie has been subjected to mowing, grazing to some extent, and abundant pocket gopher activity. The distribution of mima mounds on the upland prairie is shown in Figure 1. The mima mounds, which are widely scattered across the 65 ha of Kalsow Prairie, are numerous small circular mounds of soil ranging in diameter from 6 to 72 feet with a microrelief of from 6 to 36 inches (Fig. 3). They support a somewhat different vegetation than the surrounding prairie.

The mima mounds of Kalsow Prairie are low, rounded mounds of loose, nonstratified soil that occur most frequently on the higher, better-drained soils. Their origin is at present not well understood, but it seems that they are most likely initiated by activity of the pocket gopher (*Geomys bursarius*) and other animals. The activity of the pocket gopher on a selected 20-acre tract of the prairie is shown in Figure 4. Note the similarity in mima mound distribution on the same 20 acre unit (Fig. 5). Once initiated, the mounds might then be affected and enlarged by the differential expansion and contraction of their soils and by wind deposition of dust carried in from the adjacent cultivated fields. Continued use by pocket gophers and other burrowing mammals is evidenced by an abundance of recent soil pushed out from burrows in and about the mounds.

A vegetation analysis of several mounds picked randomly as a representative sample of the mound phenomena on the Kalsow Prairie showed that the number of plant species supported by the mounds was only slightly greater than that of the surrounding prairie (i.e., mounds = 51 species, adjacent prairie = 49 species). Of these, 38 or 75 percent of the sampled species were found in common on mounds and prairie. Those species showing cover values greater than one are placed in Table 1. Indicator species were chosen as representative of the two areas and assigned adaptation numbers according to the method of Dix and Butler (1960). This information was then used to compute Plot Index Values (PIV) for the two areas and thus separate them spatially as shown in Figure 6. The Plot Index Values were computed by use of the following equation:

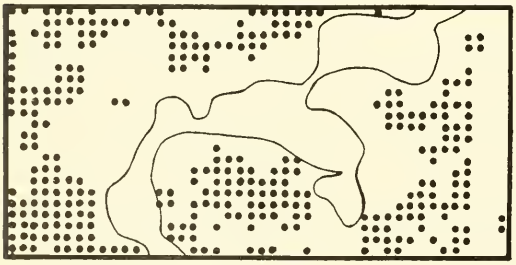


Fig. 4. Distribution of pocket gopher (*Goemys bursauzius*) activity in the 8 ha (20 acre) intensive study plot.

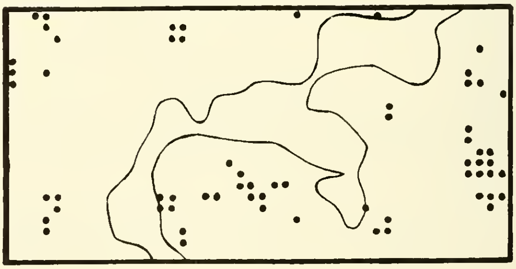


Fig. 5. Distribution of mima mound influences in the 8 ha (20 acre) intensive study plot.

$$\text{PIV} = \frac{\text{Sum (percent cover of each indicator species} \times \text{its adaptation \#)}}{\text{Sum (percent cover of each indicator species)}}$$

This spatial separation (Fig. 6) and Table 1 indicate definite differences in the vegetation of the two areas. To further strengthen the hypothesis that the vegetation changes from the mounds to the prairie, a similarity index was computed for the two areas utilizing Sorensen's (1948) index of similarity.

The value of K was calculated to be 35.2 percent, which means that the mound vegetation and the adjacent prairie vegetation have a similarity of 35 percent. Similarity values reported by Curtis (1959) for a series of communities in Wisconsin showed extremes from 34.1 to 70.3. It seems, therefore, that mound vegetation is quite distinct from that of the prairie.

The relationship of mound vegetation to adjacent prairie has not been extensively investigated (Ross et al. 1968). Attempts to describe such relationships in the present study revealed that the mounds are associated with changes in the surrounding prairie vegetation. These changes were investigated by sampling prairie vegetation adjacent to 37 of the 128 mounds studied. Two transects, one oriented north-south and the other east-west, were extended through each mound. The adjacent prairie vegetation was sampled along these transects starting at the mound boundary and extending into the prairie. Twelve samples at 12-foot intervals were taken adjacent to each mound, as shown in Figure 2. Cover estimates were recorded for each species present in the quadrat. The resulting data were analyzed by grouping all quadrats found at equal intervals from the mounds and averaging them to obtain percentage cover values for all participating species (Table 2). A similar analysis was also completed by grouping all quadrats located on the north, south, east, and west sides of the mounds and again averaging to obtain percentage cover values for all participating species (Table 3). In both cases it is evident that the mounds have provided a new microenvironment to which some prairie species respond. Some species (Table 2) show a positive response by appearing almost exclusively on the mounds or by increasing in importance from the prairie toward the mound. Species showing this type of response were *Achillea millifolium*, *Agropyron repens*, *Ambrosia artemisifolia*, *Asclepias syrica*, *Aster ericoides*, *Chenopodium album*, *Convolvulus sepium*, *Elymus canadensis*, *Fragaria virginiana*, *Galium obtusum*, *Helianthus grosseserratus*, *Helianthus laetiflorus*, *Heliopsis helianthoides*, *Oxalis stricta*, *Physalis heterophylla*, *Poa pratensis*, *Ratibida columnifera*, *Rosa suffulta*, *Solidago canadensis*, and *Spartina pectinata*. Other species showed a negative response decreasing in importance as the mound is approached from the prairie. These species were *Amorpha canescens*, *Aster laevis*, *Baptisia leucantha*, *Comandra umbellata*, *Eryngium yuccifolium*, *Lathyrus venosus*, *Liatris pycnostachya*, *Silphium laciniatum*, *Solidago rigida*, *Sporobolus heterolepis*, and *Zizia aurea*. Another response is exhibited by *Andropogon gerardi*. It increases in importance as you move toward the mound then drops

TABLE 1. Average percentage cover values in mound and adjacent prairie areas for all species with a percent cover greater than one.

	Species	% Cover (prairie)	% Cover (mounds)
[a]1	*Sporobolus heterolepis*	53.60	.04
1	*Amorpha canescens*	2.00	.83
	Schizachyrium scoparius	1.00	
2	*Zizia aurea*	1.20	.83
	Aster laevis	1.10	.04
	Solidago rigida	1.30	.10
2	*Panicum leibergii*	3.00	1.80
3	*Aster ericoides*	3.00	4.00
	Andropogon gerardi	14.00	11.85
3	*Ratibida columnifera*	1.00	2.90
	Achillea millifolium	.93	2.40
4	*Physalis heterophylla*	.04	1.90
	Rosa suffulta	.80	1.70
4	*Convolvulus sepium*	.10	1.90
	Asclepias syriaca		1.10
	Agropyron repens		1.40
	Ambrosia artemisifolia		4.30
5	*Solidago canadensis*	3.00	8.36
5	*Poa pratensis*	8.00	45.26

[a]These numbers are the adaptation numbers assigned to the different indicator species.

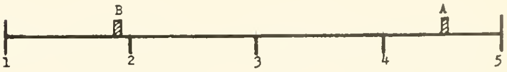


Fig. 6. Linear ordination of the mima mound and adjacent prairie vegetation according to their plot index values. A = mima mounds, B = adjacent prairie.

TABLE 2. Effects of mima mounds on cover values of the surrounding upland prairie vegetation.

		Distance from mound		
Species	Mound	12 ft	24 ft	36 ft
Achillea millifolium	.74	.50	.59	.51
Agropyron repens	1.16	.02	.02	.03
Agropyron trachycaulum	.01	.00	.00	.00
Ambrosia artemisifolia	1.91	.02	.02	.00
Ambrosia trifida	.41	.00	.00	.00
Amorpha canescens	.41	1.94	2.01	1.35
Amphicarpa bracteata	.14	.02	.00	.00
Andropogon gerardi	7.69	18.72	14.66	12.80
Anemone canadensis	.00	.00	.00	.02
Anemone cylindrica	.01	.10	.06	.02
Apocynum sibiricum	.07	.10	.00	.12
Arabis hirsuta	.01	.00	.00	.00
Artemisia ludoviciana	.61	.49	.30	.25
Asclepias sullivantii	.01	.00	.00	.00
Asclepias syriaca	1.18	.17	.02	.00
Asclepias tuberosa	.35	.51	.19	.03
Asclepias verticillata	.04	.03	.02	.00
Aster ericoides	3.96	2.23	2.50	1.82
Aster laevis	.97	1.60	1.76	.81
Aster simplex	.51	.30	.20	.24
Astragalus canadensis	.00	.02	.02	.00
Baptisia leucantha	.05	.10	.17	.02
Baptisia leucophaea	.00	.00	.10	.10
Bouteloua curtipendula	.03	.07	.05	.02
Caenothus americanus	.00	.00	.00	.10
Calamagrostis canadensis	.01	.00	.00	.02
Carex gravida	.19	.10	.07	.16
Carex aquatilis	.00	.02	.00	.00
Carex retrorsa	.00	.00	.00	.02
Chenopodium album	.77	.02	.00	.00
Cicuta maculata	.00	.00	.03	.00
Cirsium altissimum	.50	.03	.19	.15
Cirsium arvense	.25	.00	.00	.00
Comandra umbellata	.06	.23	.27	.34
Convolvulus sepium	3.13	.53	.28	.22
Desmodium canadense	1.25	2.21	1.91	1.79
Echinacea pallida	.00	.00	.00	.02
Elymus canadensis	1.22	.42	.47	.39
Elymus virginicus	.06	.00	.00	.00
Equisetum kansanum	.07	.07	.14	.07
Erigeron strigosus	.01	.00	.00	.00
Eryngium yuccifolium	.01	.10	.14	.02
Euphorbia serpyllfolia	.01	.00	.00	.00
Fragaria virginiana	.83	.79	.63	.41
Galium obtusum	.93	.74	.69	.54
Gentiana andrewsii	.00	.02	.05	.15
Helianthus grosseserratus	4.13	1.72	1.67	2.36
Helianthus laetiflorus	1.59	1.52	1.23	1.03
Helianthus maximiliani	.46	.14	.02	.00
Heliopsis helianthoides	1.32	.51	.37	.63
Juncus tenuis	.00	.02	.00	.00
Kochia scoparia	.13	.00	.00	.00
Lactuca scariola	.12	.00	.00	.02
Lathyrus palustris	.02	.00	.03	.02
Lathyrus venosus	.13	.20	.19	.07
Lespedeza capitata	.00	.02	.04	.04
Liatris aspera	.06	.02	.04	.04
Liatris pycnostachya	.01	.20	.19	.29

Table 2 coninued.

Species	Mound	Distance from mound 12 ft	24 ft	36 ft
Lithospermum canescens	.24	.57	.54	.37
Lysimachia chiliata	.08	.03	.02	.03
Lysimachia hybrida	.00	.10	.02	.10
Lysimachia quadriflora	.00	.00	.02	.02
Muhlenbergia racemosa	.40	.51	.69	.39
Oenothera biennis	.11	.00	.00	.00
Oxalis stricta	1.42	.08	.02	.02
Panicum capillare	.27	.00	.00	.00
Panicum leibergii	2.02	3.13	3.89	2.52
Panicum virgatum	.62	.52	.39	.54
Pedicularis canadensis	.00	.00	.02	.03
Petalostemum candidum	.02	.19	.10	.25
Petalostemum purpureum	.02	.25	.35	.20
Phleum pratensis	.01	.00	.03	.03
Phlox pilosa	.19	.25	.41	.20
Physalis heterophylla	1.24	.12	.08	.02
Physalis virginiana	.35	.10	.14	.07
Poa pratensis	40.47	10.14	7.64	6.69
Polygonum convolvulus	.14	.00	.00	.00
Polygonum ramosissimum	.09	.00	.00	.00
Potentilla arguta	.09	.00	.10	.02
Psoralea argophylla	.15	.14	.24	.10
Pycnanthemum virginianum	.00	.07	.00	.19
Ratibida columnifera	3.08	2.19	1.30	1.49
Rosa suffulta	2.48	1.20	1.49	1.50
Schizachyrium scoparium	.01	1.37	.42	.46
Scutellaria leonardii	.03	.03	.04	.02
Senecio pauperculus	.13	.03	.03	.14
Setaria lutescens	.62	.00	.02	.00
Setaria viridis	.03	.00	.00	.00
Silphium laciniatum	.02	.39	.54	.69
Solanum nigrum	.09	.00	.00	.00
Solidago canadensis	10.73	5.03	3.80	4.51
Solidago gymnospermoides	.00	.02	.00	.02
Solidago missouriensis	.11	.23	.35	.20
Solidago rigida	.47	1.37	2.50	1.47
Sorghastrum nutans	.00	.10	.27	.65
Spartina pectinata	.94	.37	.32	.24
Sporobolus heterolepis	1.05	22.61	31.00	33.97
Stipa spartea	.25	.59	.89	.49
Taraxacum officinale	.00	.10	.00	.00
Thalictrum dasycarpum	.01	.00	.00	.00
Tradescantia bracteata	.01	.00	.00	.00
Trifolium pratense	.05	.00	.02	.00
Viola pedatifida	.19	.27	.19	.27
Viola sp.	.13	.07	.10	.05
Vicia americana	.11	.30	.07	.14
Zizia aurea	1.44	2.08	2.47	1.65

sharply in average percentage cover as you reach the mound proper. Other species showing this same kind of response were *Schizachyrium scoparius, Bouteloua curtipendula, Desmodium canadense,* and *Lithospermum canescens.*

Evidence from Table 3 indicates that several species also showed some response to small differences in microrelief as associated with aspect. Species showing preference for the southern aspect were *Amorpha canescens, Schizachyrium scoparius, Asclepias tuberosa, Aster ericoides, Comandra umbellata, Lithospermum canescens, Panicum leibergii, Petalostemum candidum, Poa pratensis, Solidago missouriensis,* and *Stipa*

Table 3. Effects of mima mounds on cover values of the surrounding upland prairie vegetation in relation to aspect.

Species	Mound	North	South	East	West
Achillea millifolium	.74	.56	.38	.68	.56
Agropyron repens	1.16	.02	.00	.05	.02
Ambrosia artemisifolia	1.91	.02	.02	.00	.00
Amorpha canescens	.41	2.16	2.68	1.24	2.07
Amphicarpa bracteata	.41	.00	.00	.02	.00
Andropogon gerardi	7.69	16.24	15.16	16.64	13.22
Anemone canadensis	.00	.00	.00	.02	.00
Anemone cylindrica	.01	.11	.05	.07	.05
Apocynum sibiricum	.07	.11	.00	.07	.00
Artemisia ludoviciana	.61	.36	.25	.45	.34
Asclepias syriaca	1.18	.16	.05	.00	.02
Asclepias tuberosa	.35	.14	.74	.02	.11
Asclepias verticillata	.04	.02	.00	.02	.02
Aster ericoides	3.96	2.09	2.52	2.00	2.17
Aster laevis	.97	1.31	1.31	1.62	1.55
Aster simplex	.51	.14	.11	.27	.47
Astragalus canadensis	.00	.05	.00	.00	.00
Baptisia leucantha	.05	.00	.00	.29	.14
Bouteloua curtipendula	.03	.02	.02	.09	.05
Calamagrostis canadensis	.01	.11	.00	.02	.00
Carex brevoir	.19	.00	.11	.23	.05
Carex aquatilix	.00	.00	.02	.00	.00
Carex lasiocarpa	.00	.00	.00	.02	.00
Chenopodium album	.77	.00	.00	.00	.02
Cicuta maculata	.00	.00	.00	.00	.05
Cirsium altissimum	.50	.09	.07	.07	.20
Comandra umbellata	.06	.20	.50	.45	.23
Convolvulus sepium	3.13	.63	.25	.23	.47
Desmodium canadense	1.25	1.78	1.91	1.89	2.16
Echinacea pallida	.00	.00	.02	.02	.00
Elymus canadensis	1.22	.43	.63	.45	.25
Equisetum kansanum	.07	.11	.11	.09	.07
Eryngium yuccifolium	.01	.05	.00	.14	.14
Fragaria virginiana	.83	.59	.70	.68	.65
Galium obtusum	.93	.88	.86	.52	.68
Gentiana andrewsii	.00	.05	.14	.02	.05
Helianthus grosseserratus	4.13	2.41	2.18	2.09	1.01
Helianthus laetiflorus	1.59	.97	1.26	1.58	1.22
Helianthus maximiliani	.46	.16	.00	.05	.02
Heliopsis helianthoides	1.32	.43	.52	.92	.27
Juncus tenuis	.00	.00	.00	.02	.00
Lactuca scariola	.12	.02	.00	.00	.00
Lathyrus palustris	.02	.02	.00	.05	.02
Lathyrus venosus	.13	.07	.14	.23	.05
Lespedeza capitata	.00	.07	.00	.07	.02
Liatris aspera	.06	.00	.02	.09	.05
Liatris pycnostachya	.01	.16	.29	.23	.27
Lithospermum canescens	.24	.43	.74	.41	.45
Lysimachia chiliata	.08	.00	.05	.05	.02
Lysimachia hybrida	.00	.00	.16	.02	.00
Lysimachia quadriflora	.00	.00	.00	.02	.02
Muhlenbergia racemosa	.40	.56	.47	.36	.79
Oxalis stricta	1.42	.02	.02	.07	.05
Panicum leibergii	2.02	2.97	4.35	2.57	2.68
Panicum virgatum	.62	.36	.63	.65	.41
Pedicularis canadensis	.00	.00	.00	.05	.05
Petalostemum candidum	.02	.18	.27	.14	.11

Table 3 continued.

Species	Mound	North	South	East	West
Petalostemum purpureum	.02	.14	.16	.52	.29
Phleum pratense	.01	.05	.02	.02	.02
Phlox pilosa	.19	.34	.18	.45	.20
Physalis heterophylla	1.24	.00	.14	.11	.23
Physalis virginiana	.35	.14	.07	.16	.14
Poa pratensis	40.47	7.55	9.89	7.76	6.42
Potentilla arguta	.09	.02	.02	.14	.00
Psoralea argophylla	.15	.09	.20	.32	.09
Pycnanthemum virginianum	.00	.05	.05	.05	.07
Ratibida columnifera	3.08	1.37	1.80	2.00	1.60
Rosa suffulta	2.48	1.55	1.55	.83	1.22
Schizachyrium scoparium	.01	.45	1.28	.86	.45
Scutellaria leonardii	.03	.05	.02	.07	.02
Senecio pauperculus	.13	.18	.02	.07	.05
Setaria lutescens	.62	.00	.02	.00	.00
Silphium laciniatum	.02	.29	.61	.36	.90
Solidago canadensis	10.73	5.50	4.28	4.12	4.08
Solidago gymnospermoides	.00	.00	.00	.07	.00
Solidago missouriensis	.11	.20	.52	.27	.11
Solidago rigida	.47	1.94	1.64	1.46	2.03
Sorghastrum nutans	.00	.95	.14	.16	.27
Spartina pectinata	.94	.14	.45	.56	.25
Sporobolus heterolepis	1.05	32.30	27.03	24.28	36.03
Stipa spartea	.25	.18	.50	.38	.38
Taraxacum officinale	.00	.14	.00	.00	.00
Trifolium pratense	.05	.00	.00	.02	.00
Viola pedatifida	.19	.27	.27	.29	.16
Viola sp.	.13	.07	.09	.02	.14
Vicia americana	.11	.36	.18	.09	.14
Zizia aurea	1.44	2.45	2.05	2.30	2.36

spartea. Species showing preference for the north side of the mounds were *Anemone cylindrica, Asclepias syriaca, Convolvulus sepium, Sorghastrum nutans*, and *Vicia americana*.

It seems the mounds, however slight in microrelief, provide sufficient modification of the prairie to allow striking patterns of vegetational change to emerge. In one aspect the mounds provide habitats that exhibit different levels of disturbance (i.e., the amount of actual disturbance decreases as you leave the mound and proceed into the prairie). The response of several species to the disturbance factor would tend to support the hypothesis that in the Kalsow prairie the changes that have occurred since 1953 are in effect caused by some degree of disturbance. Several of the species that showed increased importance since Moyer's (1953) work (i.e., *Solidago canadensis, Panicum leibergii, Helianthus grosseserratus, Desmodium canadense, Galium obtusum*, and *Fragaria virginiana*) also showed a corresponding increase in importance as you approach the mounds from the prairie. Likewise, some of the species which decreased in importance in the past 16 years (i.e., *Zizia aurea, Sorghastrum nutans*, and *Sporobolus heterolepis*) decreased as disturbance increased. Several species, *Andropogon gerardi, Schizachyrium scoparius, Bouteloua curtipendula*, and *Lithospermum canescens*, indicated positive response to slight disturbance but negative response to heavier disturbance.

It seems, therefore, that mounds or other forms of disturbance affect vegetation changes in the prairie which, when considered over a period of years, may alter the original structure and composition of its vegetation. Whether such changes would be permanent or temporary is a question that can be answered only by long-term studies set up to follow the fluctuations of the prairie vegetation and its environment.

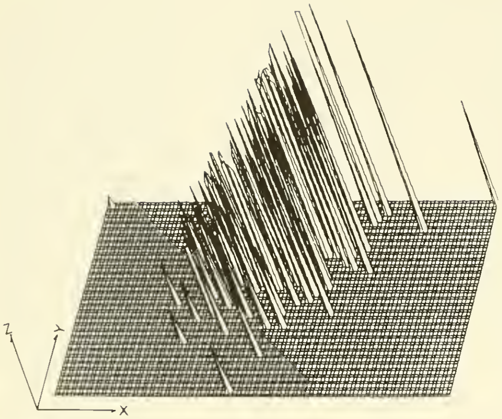


Fig. 7. Three-dimensional ordination of 128 mima mounds found in Kalsow Prairie.

Analysis of the mound vegetation as a unit was attempted using Orloci's (1966) method of ordination. Each mound was considered as a stand of vegetation and all 128 mounds were projected into three-dimensional space (Fig. 7). This analysis placed the 128 mounds into a relatively linear relationship in the X, Y, and Z planes (Fig. 7). This indicated that only two to three factors could be responsible for the placing of each mound into this sort of an alignment in relation to all the other mounds. Further study indicated that alignment was closely related to the two species *Poa pratensis* and *Solidago canadensis*. *Poa pratensis* was responsible for alignment of the X-axis (Fig. 8) and *Solidago canadensis* was responsible for alignment of the Y-axis (Fig. 9). Because no environmental measurements were taken, it was impossible to determine the causative factors to which these two species were linked. It appears, however, that the vegetation of the mounds fits the concept of a continuum and that perhaps the controlling environmental factors would be related to the age of the mound and the degree of disturbance.

Poa pratensis, for example, is an introduced species whose characteristics are such that it is able to compete well within the environment of the prairie protected from early spring fires. Under conditions of grazing, mowing, and other disturbance, *Poa pratensis* is known to increase in importance (Weaver 1954).

By ordinating the species of the mounds into three-dimensional space (Fig. 10), it was found that only those species having irregular distribution patterns were isolated. The most important species were *Poa pratensis, Solidago canadensis, Solanum nigrum, Andropogon gerardi, Aster ericoides, Helianthus grosseserratus, Connvolvulus sepium, Helianthus laetiflorus, Desmodium canadense, Ambrosia artemisifolia, Panicum leibergii, Ratibida columnifera, Rosa suffulta,* and *Zizia aurea*. Again it was found that the two species *Poa pratensis* and *Solidago canadensis* were responsible for alignment of the X and Y-axes.

To further understand the relationships of mound vegetation, interspecific association values were computed for all possible pairs of species (Table 4). Out of 7200 possible combinations only 78, or about 1 percent, showed any degree of positive association. Basic clusters or groups of species within these 78 positive association units are illustrated in Figures 11 and 12.

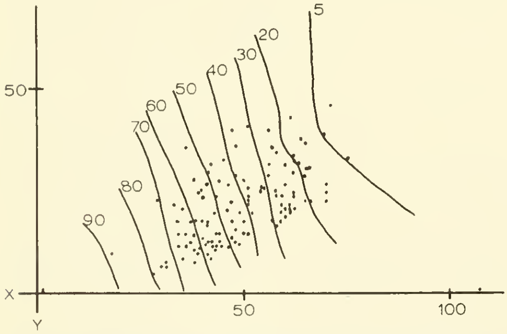


Fig. 8. Two-dimensional ordination of mima mounds with percentage cover values of *Poa pratensis* shown relating indirectly to the X-axis.

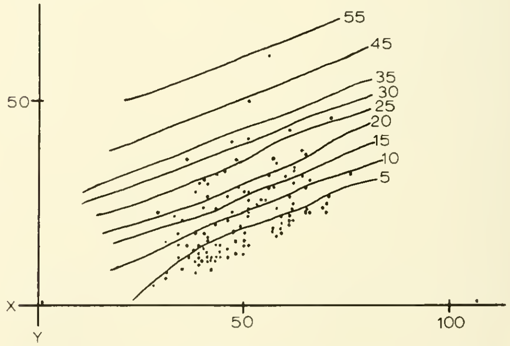


Fig. 9. Two-dimensional ordination of mima mounds with percentage cover values of *Solidago canadensis* shown relating indirectly to the Y-axis.

Five of the six clusters (B through F) shown in Figure 11 are composed of species that are generally tolerant of disturbance and were shown to be most important on the mound itself (Table 2). Cluster A (Fig. 11) is composed of upland prairie species. Figure 12 shows four clusters that are designated as A, B, C, and D. Cluster A has as its center *Solidago canadensis* and as associated species *Carex gravida, Monarda fistulosa, Senecio pauperculus, Aster simplex, Solanum nigrum,* and *Apocynum sibiricum.* Cluster B has for its center a unit of three species: *Desmodium canadense, Fragaria virginiana,* and *Helianthus grosseserratus.* These are then associated with *Galium obtusum* and several other species only on a very limited basis (i.e., 20 to 40 percent). Cluster C has as its center *Zizia aurea* and as associated species: *Lythrum alatum, Pedicularis canadensis,* and *Petalostemum candidum.* Here again *Zizia aurea* and its associated species are weakly associated with several other species as well as to cluster D. Cluster D is basically a discrete unit including *Lycopus americanus, Lysimachia chiliata,* and *Spartina pectinata.* In all cases the clusters of Figure 12 appear to be composed of species generally found on lowland prairie soils or bordering potholes and drainage ways. This would indicate that the mound environment as shown by these groups might be somewhat more moist than the adjacent prairie.

Specifically, the interspecific association analyses indicate two groups of species occupying the mima mounds of Kalsow prairie.

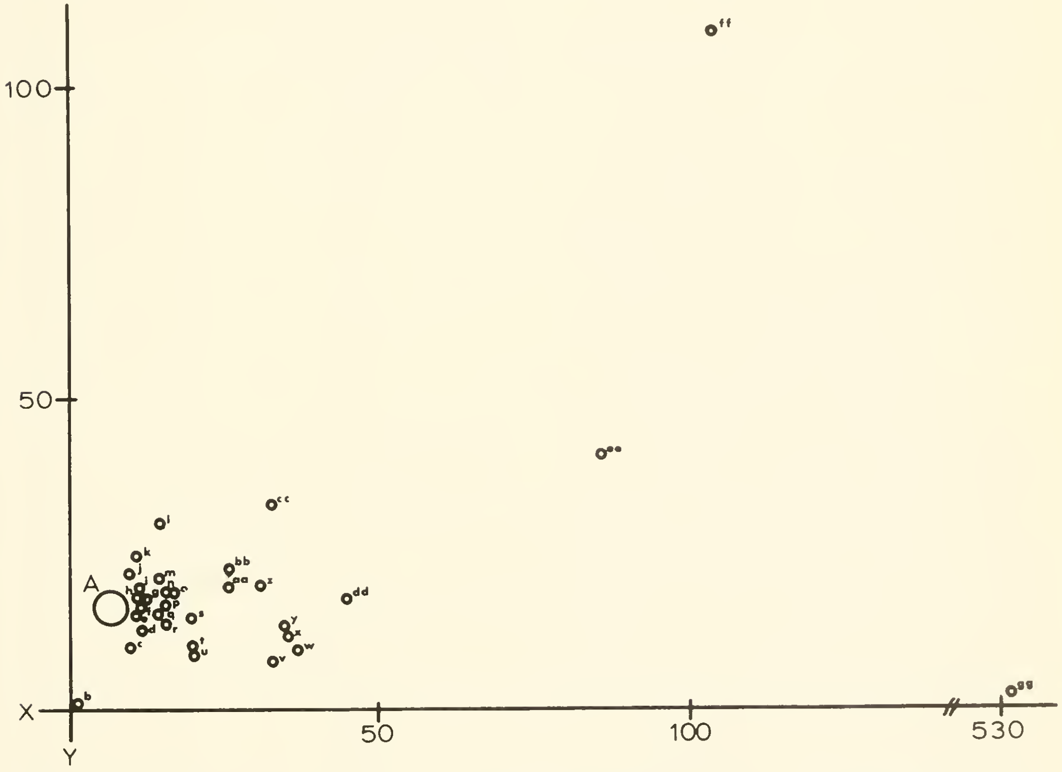


Fig. 10. Two-dimensional ordination of species found in the mima mound study; A = cluster of species not showing distinct distribution patterns, b = *Solanum nigrum,* c = *Ambrosia trifida,* d = *Agropyron repens,* e = *Amorpha canescens,* f = *Chenopodium album,* g = *Fragaria virginiana,* h = *Achillea millifolium,* i = *Asclepias syriaca,* j = *Spartina pectinata,* k = *Panicum virgatum,* l = *Zizia aurea,* m = *Heliopsis helianthoides,* n = *Physalis heterophylla,* o = *Elymus canadensis,* p = *Aster laevis,* q = *Oxalis stricta,* r = *Artemisia ludoviciana,* s = *Sporobolus heterolepis,* t = *Aster simplex,* u = *Galium obtusum,* v = *Ambrosia artemisifolia,* w = *Convolvulus sepium,* x = *Helianthus laetiflorus,* y = *Desmodium canadense,* z = *Ratibida columnifera,* aa = *Panicum leibergii,* bb = *Rosa suffulta,* cc = *Helianthus grosseserratus,* dd = *Aster ericoides,* ee = *Andropogon gerardi,* ff = *Solidago canadensis,* gg = *Poa pratensis.*

TABLE 4. Cole's Index values expressing positive interspecific association in mima mound communities.

Species	Species	X^2[a]	C_7[b]	G_7[c]
Agropyron repens	*Convolvulus sepium*	48.20	.45	.06
Amorpha canescens	*Panicum leibergii*	37.20	.49	.07
	Sporobolus heterolepis	24.82	.19	.03
Andropogon gerardi	*Poa pratensis*	8.82	.63	.21
Apocynum sibiricum	*Solidago canadensis*	5.04	.33	.14
	Spartina pectinata	15.77	.21	.05
Artemisia ludoviciana	*Convolvulus sepium*	16.97	.19	.04
Asclepias tuberosa	*Panicum virgatum*	12.68	.17	.04
Aster laevis	*Panicum leibergii*	23.91	.19	.03
Aster simplex	*Elymus canadensis*	5.99	.19	.07
	Helianthus grosseserratus	54.44	.35	.04
	Ratibida columnifera	8.92	.17	.05
	Solidago canadensis	17.50	.45	.11
Bouteloua curtipendula	*Convolvulus sepium*	3.80	.36	.18
	Lithospermum canescens	14.34	.23	.06
	Panicum leibergii	4.13	.30	.14
	Phlox pilosa	9.26	.21	.07
	Zizia aurea	4.10	.21	.10
Carex gravida	*Fragaria virginiana*	3.91	.19	.09
	Physalis virginiana	17.76	.25	.05
	Solidago canadensis	7.54	.65	.23
Chenopodium album	*Elymus canadensis*	7.69	.18	.06
Cirsium altissimum	*Panicum capillare*	39.39	.17	.02
Comandra umbellata	*Desmodium canadense*	14.88	.20	.05
	Fragaria virginiana	17.87	.26	.06
	Calium obtusum	22.35	.29	.06
	Panicum leibergii	10.20	.32	.09
	Sporobolus heterolepis	28.49	.25	.04
Desmodium canadense	*Fragaria virginiana*	230.53	.45	.02
	Galium obtusum	239.96	.46	.02
	Helianthus grosseserratus	75.32	.29	.03
	Panicum virgatum	55.13	.17	.02
	Ratibida columnifera	20.91	.19	.04
	Solidago canadensis	8.52	.22	.07
	Spartina pectinata	79.85	.24	.02
	Zizia aurea	87.88	.31	.03
Equisetum kansanum	*Helianthus laetiflorus*	13.69	.34	.09
Eryngium yuccifolium	*Viola pedatifida*	75.09	.82	.09
Fragaria virginiana	*Galium obtusum*	137.95	.30	.02
	Helianthus grosseserratus	71.48	.24	.02
Galium obtusum	*Helianthus grosseserratus*	72.33	.24	.02
	Panicum virgatum	75.68	.17	.01
	Zizia aurea	68.88	.24	.02
Helianthus maximiliani	*Panicum leibergii*	4.31	.23	.11
Kochia scoparia	*Physalis heterophylla*	9.38	.42	.13
Lactuca scariola	*Phlox pilosa*	5.36	.17	.07
Lathyrus palustris	*Ratibida columnifera*	5.58	.36	.15
	Solidago rigida	5.68	.19	.08
Liatris pycnostachya	*Lithospermum canescens*	19.50	.36	.08
	Petalostemum purpureum	23.57	.19	.03
	Psoralea argophylla	11.75	.18	.05
	Solidago rigida	7.77	.25	.08
	Sporobolus heterolepis	6.69	.24	.09
Lithospermum canescens	*Panicum leibergii*	16.28	.25	.06
Lycopus americanus	*Lysimachia chiliata*	145.04	.66	.05
	Spartina pectinata	9.46	.62	.20

[a] Chi-square

[b] Cole's Index

[c] Standard deviation Cole's Index

TABLE 4. Cole's Index values expressing positive interspecific association in mima mound communities.

Species	Species	X^2[a]	C_7[b]	G_7[c]
Lysimachia chiliata	*Spartina pectinata*	40.75	.60	.09
	Zizia aurea	12.21	.40	.11
Lythrum alatum	*Zizia aurea*	20.90	.70	.15
Monarda fistulosa	*Solidago canadensis*	5.17	1.00	.43
Oenothera biennis	*Panicum capillare*	102.87	.33	.03
Panicum virgatum	*Solidago canadensis*	20.30	.37	.08
	Spartina pectinata	27.11	.15	.02
Pedicularis canadensis	*Zizia aurea*	26.42	1.00	.19
Petalostemum candidum	*Zizia aurea*	10.36	.30	.09
Polygonum ramosissimum	*Rumex crispus*	71.91	.22	.02
Potentilla arguta	*Viola pedatifida*	7.62	.17	.06
Senecio pauperculus	*Solidago canadensis*	6.56	.70	.27
	Solidago rigida	4.90	.17	.07
	Spartinia pectinata	10.20	.31	.09
	Zizia aurea	8.91	.36	.12
Silphium laciniatum	*Solidago rigida*	7.60	.19	.06
	Spartina pectinata	11.51	.30	.08
	Viola sp.	97.96	.42	.04
	Zizia aurea	9.31	.33	.10
Solanum nigrum	*Solidago canadensis*	4.29	.51	.24
Solidago rigida	*Zizia aurea*	23.58	.19	.03
Viola sp.	*Zizia aurea*	17.37	.30	.06

[a] Chi-square
[b] Cole's Index
[c] Standard deviation Cole's Index

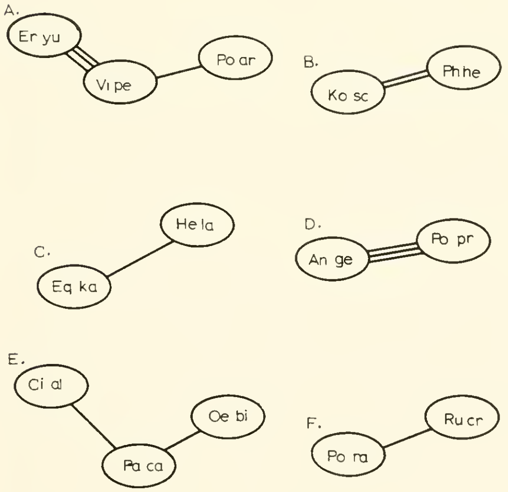


Fig. 11. Association of species found in the mima mound study, Kalsow Prairie, as determined by Cole's (1949) Index, the more lines between species, the greater the association; (A) Er yu = *Eryngium yuccifolium*, Vi pe = *Viola pedatifida*, Po ar = *Potentilla arguta*, (B) Ko sc = *Kochia scoparia*, Ph he = *Physalis heterophylla*, (C) Eq ka = *Equisetum kansanum*, He la = *Helianthus laetiflorus*, (D) An ge = *Andropogon gerardi*, Po pr = *Poa pratensis*, (E) Ci al = *Circium altissimum*, Pa ca = *Panicum capillare*, Oe bi = *Oenothera biennis*, (F) Po ra = *Polygonum ramosissimum*, Ru cr = *Rumex crispus*.

Those that are tolerant to disturbance and are found occupying the central portions of the mound proper (Fig. 11) and those that are characteristic of lowland prairie areas and are more important at the edges and lower slopes of the mounds. We could find no indication that these groups were associated with mound size.

It appears that once a mound is formed, a new microenvironment is created that affects directly the structure and stability of the surrounding prairie. This effect is shown in the response of many species to the creation of these new habitats. The factors deemed most influential in affecting these new habitats are disturbance and microrelief. Field observations indicate that the mounds represent microsuccession sites and cause changes in the prairie vegetation to earlier stages in the sere. This hypothesis is supported by the fact that, in all cases studied, the vegetation of the mounds included a number of weed species (annuals, biennials, and some perennials) that are recognized as pioneer species. The resulting mound vegetation appears to be made up of a mixture of these pioneer species and species from the prairie that respond favorably to mound disturbance. Present evidence also indicates that mound vegetation is

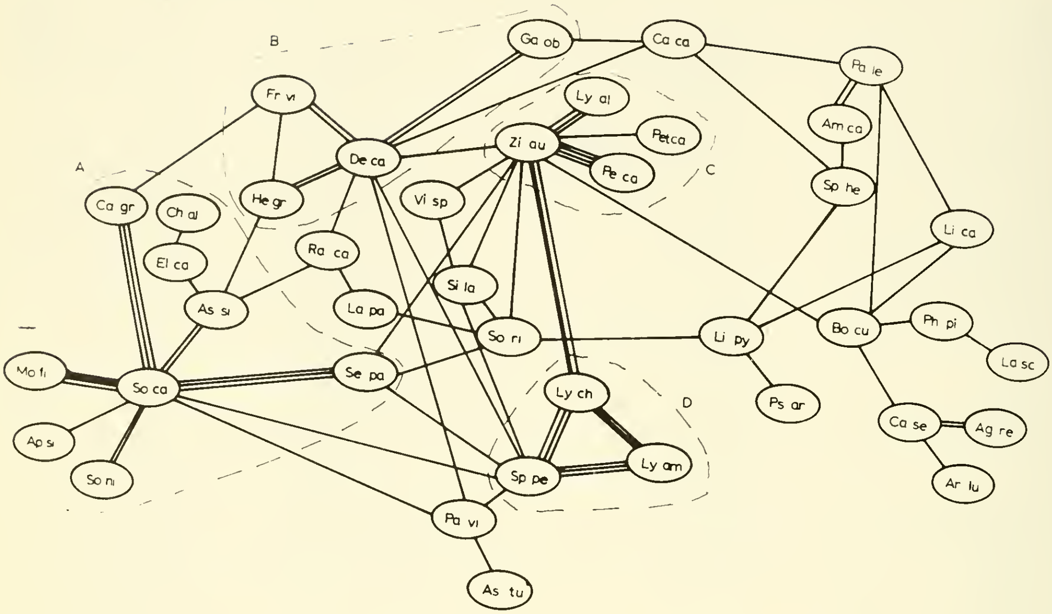


Fig. 12. Association of species found in the mima mound study, Kalsow Prairie, as determined by Cole's (1949) Index, the more lines between species, the greater the association; groups A, B, C, and D are basic clusters; Ag re = *Agropyron repens*, Am ca = *Amorpha canescens*, Ap si = *Apocynum sibiricum*, Ar lu = *Artemisia ludoviciana*, As si = *Aster simplex*, As tu = *Asclepias tuberosa*, Bo cu = *Bouteloua curtipendula*, Ca ca = *Calamagrostis canadensis*, Ca gr = *Carex gravida*, Ch al = *Chenopodium album*, Co se = *Convolvulus sepium*, De ca = *Desmodium canadense*, El ca = *Elymus canadensis*, Fr vi = *Fragaria virginiana*, Ga ob = *Galium obtusum*, He gr = *Helianthus grosseserratus*, Mo fi = *Monarda fistulosa*, Pa le = *Panicum leibergii*, Pa vi = *Panicum virgatum*, Pe ca = *Pedicularis canadensis*, Pet ca = *Petalostemum candidum*, Ph Pi = *Phlox pilosa*, Ps ar = *Psoralea argophylla*, La pa = *Lathyrus palustris*, La sc = *Lactuca scariola*, Li ca = *Lithospermum canescens*, Li py = *Liatris pycnostachya*, Ly al = *Lythrum alatum*, Ly am = *Lycopus americanus*, Ly ch = *Lysimachia chiliata*, Ra co = *Ratibida columnifera*, Se pa = *Senecio pauperculus*, Si la = *Silphium laciniatum*, Sp he = *Sporobolus heterophylla*, Sp pe = *Spartina pectinata*, So ni = *Solanum nigrum*, So ca = *Solidago canadensis*, So ri = *Solidago rigida*, Vi sp = *Viola* sp., Zi au = *Zizia aurea*.

undergoing succession that may be repeatedly set back by more disturbance. It seems that mound vegetation is strongly influenced in its basic composition by the adjacent prairie flora.

LITERATURE CITED

AIKMAN, J. M. 1959. Prairie research in Iowa. American Biology Teacher 21:7–8.

AIKMAN, J. M., AND R. F. THORNE. 1956. The Cayler Prairie: an ecologic and taxonomic study of a northwest Iowa prairie. Iowa Acad. of Sci. 63:177–200.

BRENNAN, K. M. 1969. Vertebrate fauna of Kalsow Prairie. Unpublished thesis. Iowa State Univ., Ames, Iowa.

BROTHERSON, J. D. 1969. Species composition, distribution, and phytosociology of Kalsow Prairie, a mesic tall-grass prairie in Iowa. Unpublished dissertation. Iowa State Univ., Ames, Iowa. 196 pp.

______. 1980. Zonation patterns in the potholes of Kalsow Prairie, Iowa. Great Basin Nat. 40:327–384.

BROTHERSON, J. D., AND R. Q. LANDERS. 1976. Recover from severe grazing in an Iowa tall-grass prairie. Pages 51–56 *in* D. C. Glenn-Lewis and R. Q. Landers, eds., Proc. Fifth Midwest Prairie Conference. Iowa State Univ., Ames, Iowa.

CAIN, S. A., AND F. C. EVANS. 1952. The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contributions from the Laboratory of Vertebrate Biology No. 52.

COLE, L. C. 1949. The measurement of interspecific association. Ecology 30:411–424.

Collins, B. 1975. Range vegetation and mima mounds in north Texas. J. Range Manag. 28:209–211.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–66.

Davids, R. C. 1967. The mystery of mima mounds. Farm Journal 91:17–19.

Del Moral, R., and D. C. Deardorff. 1976. Vegetation of the mima mounds, Washington State. Ecology 57:520–530.

Dix, R. L., and J. E. Butler. 1960. A phytosociological study of a small prairie in Wisconsin. Ecology 41:316–327.

Ehrenreich, J. H. 1957. Management practices for maintenance of native prairies in Iowa. Unpublished dissertation. Iowa State Univ., Ames, Iowa.

Esau, K. L. 1968. Carabidae (Coleoptera) and other arthropods collected in pitfall traps in Iowa cornfields, fencerows, and prairies. Unpublished dissertation. Iowa State Univ., Ames, Iowa.

Gilly, C. L. 1946. The Cyperaceae of Iowa. Iowa State Coll. J. Sci. 21:55–151.

Gleason, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Lancaster, Pennsylvania, Lancaster Press, Inc. 3 vol.

Hansen, R. M. 1962. Movements and survival of *Thomomys talpoides* in a mima mound habitat. Ecology 43:151–154.

Hayden, Ada. 1943. A botanical survey in the Iowa lake region of Clay and Palo Alto counties. Iowa State Coll. J. Sci. 17:277–416.

———. 1945. The selection of prairie areas in Iowa which should be preserved. Proc. Iowa Acad. Sci. 52:127–148.

———. 1946. A progress report on the preservation of prairie. Proc. Iowa Acad. Sci. 53:45–82.

Kennedy, R. K. 1969. An analysis of tall-grass prairie vegetation relative to slope position, Sheeder Prairie, Iowa. Unpublished thesis. Iowa State Univ., Ames, Iowa.

Landers, R. W. 1966. Visit the virgin prairie. Iowa Farm Science 21:418–419.

McGinnies, W. J. 1960. Effect of mima type microrelief on herbage production of five seeded grasses in western Colorado. J. Range Manag. 13:231–239.

Mielke, H. W. 1977. Mound building by pocket gophers (Geomydoe): their impact on soils and vegetation in North America. J. Biogeography 4:171–180.

Moyer, J. F. 1953. Ecology of native prairie in Iowa. Unpublished dissertation. Iowa State Univ., Ames, Iowa.

Norton, D. C., and P. E. Ponchillia. 1968. Stylet-bearing nematodes associated with plants in Iowa prairies. J. Iowa Acad. Sci. 75:32–35.

Orloci, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. J. Ecology 54:193–215.

Pohl, R. W. 1966. The grasses of Iowa. Iowa State J. Science 40:341:566.

Richards, M. S. 1969. Observations on responses of prairie vegetation to an April fire in central Iowa. Unpublished thesis. Iowa State Univ., Ames, Iowa.

Ross, B. A., J. R. Tester, and W. J. Breckenridge. 1968. Ecology of mima-type mounds in northwestern Minnesota. Ecology 49:172–177.

Ruhe, R. V. 1969. Quaternary landscapes in Iowa. Iowa State Univ. Press, Ames, Iowa. 249 pp.

Rydberg, P. A. 1931. A short phytogeography of the prairies and great plants of central North America. Brittonia 1:57–66.

Scheffer, V. B. 1947. The mystery of the mima mounds. Sci. Monthly 65:283–294.

———. 1958. Do fossorial rodents originate mima-type microrelief? American Midland Naturalist 59:505–510.

Schmitt, D. P. 1969. Plant parasitic nematodes and nematode populations in the Kalsow Prairie. Unpublished thesis. Iowa State Univ., Ames, Iowa.

Shimek, B. 1911. The prairies. Bull. Lab. Nat. Hist., State Univ. Iowa 6:169–240.

———. 1915. The plant geography of the Lake Okoboji region. Bull. Lab. Nat. Hist., State Univ. of Iowa 7:1–90.

———. 1925. The persistence of the prairie. Univ. of Iowa Studies 11:3–24.

Sorensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. Biol. Rev. 23:411–488.

Steiger, T. L. 1930. Structure of prairie vegetation. Ecology 11:170–217.

Tester, J. R., and W. H. Marshall. 1961. A study of certain plant and animal interrelations on a native prairie in northwestern Minnesota. Minnesota Museum of Natural History. Occasional Papers No. 8:1–50.

Thorp, J. 1949. Effects of certain animals that live in the soil. Sci. Monthly 68:180–191.

Weaver, J. E. 1930. Underground plant development in its relation to grazing. Ecology 11:543–557.

———. 1954. North American Prairie. Johnsen Publishing Company, Lincoln, Nebraska. 348 pp.

Weaver, J. E., and T. J. Fitzpatrick. 1932. Ecology and relative importance of the dominants of the tall-grass prairie. Bot. Gaz. 93:113–50.

———. 1934. The prairie. Ecol. Monogr. 4:109–295.

OCCURRENCE AND EFFECT OF *CHRYSOMYXA PIROLATA* CONE RUST ON *PICEA PUNGENS* IN UTAH

David L. Nelson[1] and Richard G. Krebill[2]

Abstract.— In a rare 1969 epidemic, spruce cone rust caused by *Chrysomyxa pirolata* infected 40–100 percent of trees and 20–67 percent of cones on riparian Colorado blue spruce on plots located in a 2200–2400 m elevational zone in Huntington Canyon of central Utah. Uredinial and telial sporulation on *Pyrola* spp. began in mid-June, a time closely correlated with opening of pistillate spruce cones. Cone phenology and host habitat, as influenced by elevation, are apparently important factors in the restricted niche of the cone rust fungus in Utah. Several preceding consecutive years with extended periods of spring and fall moisture were associated with occurrence of the epidemic, although no cause-and-effect relationship was established. Weather records indicate that these events are infrequent in this climatic zone, and there was no detectable recurrence of cone rust for at least 9 years following 1969. Outwardly normal seeds developed in diseased cones, but seed germinability was reduced by 25 percent. Aecial spore masses between cone scales, cone resinosis, and distortion of cone scales prevented seed dispersal to the extent that the seed crop was effectually destroyed.

Our discovery of a rare outbreak of spruce cone rust caused by *Chrysomyxa pirolata* (Körnike) Wint. on *Picea pungens* Engelm. in central Utah (Nelson and Krebill 1970) afforded the opportunity to study the nature of the disease. Mycological collection records provide insight into its distribution; but information on the effect, ecological nature, and epidemiology of the disease is limited, especially for the contiguous western United States.

Review

The spruce cone rust fungus is heteroecious and full cycled (Fraser 1912, Savile 1953, Ziller 1974). The aecial and pycnial stages form on female cones of *Picea* spp. Peridermial aecia develop on outer surfaces of cone scales (Arthur and Kern 1906). Mycelium of the uredinial and telial stages is systemic and perennial in *Pyrola* and *Moneses* spp. (Rice 1927, Gäumann 1959). The perennial nature ensures persistence of the rust during periods unfavorable for infection (Savile 1953).

Favorable habitat for *C. pirolata* occurs primarily in the boreal regions of the northern hemisphere (Jørstad 1940, Savile 1950, Ziller 1974), extending across North America and Eurasia. In the contiguous western United States, incidence is relatively low, and on spruce considered only occasional (Hedgcock 1912) compared with Canada, where its occurrence is frequent (Can. Dept. Environ. 1951–1975). Abundance similar to that in Canada is evident in Alaska (Cash 1953, Kimmey and Stevenson 1957, Zasada and Gregory 1969), and it occurs on *Pyrola* (pyrola) or *Moneses* (single-delight) species in Nevada (Arthur 1907–1931), California, Colorado, Idaho, Oregon, Montana, New Mexico, Utah, Washington, Wyoming (Arthur 1934), South Dakota (Peterson 1961), and Arizona (Gilbertson and McHenry 1969). As in other regions of its distribution (Ziller 1974), in the western United States in certain areas, it is rather common on *Pyrola* and *Moneses* spp., but not known on spruce. Prior to this account, *C. pirolata* was known to occur on spruce in Colorado, Montana, Oregon (Arthur 1934), and Washington (Shaw 1973). Apparent extension beyond the range of spruce may result from its perennial nature on the telial host and a possible lower frequency of critical requirements occurring for infection of spruce than for pyrola. Although unclear from the literature, however, it appears that collection locations of the rust on *Pyrola* and *Moneses* spp. in the West are within the distributional range of spruce. Presently a clear extension beyond the range of spruce is the occurrence in Guatemala on *Pyrola secunda* L. (Cummins 1943), a great distance from the nearest indigenous spruce in northern Mexico (Martínez 1963). During the Pleistocene, spruce extended farther south and the fungus may have survived on pyrola to the present, when spruce died out, rather than spreading southward on pyrola. Inaccessibility of rusted cones to the casual collector is likely a factor in the apparent low frequency of this rust on spruce. Also, there are no specific, systematic annual surveys made in the western United States to detect rust diseases as there are in Canada.

---

[1] Intermountain Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Ogden, Utah, located at Shrub Sciences Laboratory, Provo, Utah 84601.

[2] Rocky Mountain Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory, Arizona State University, Tempe, Arizona 85281.

Little knowledge of the epidemiology of this fungus exists. Clinton and McCormick (1919), in Petri dish culture tests, failed to obtain infection of excised pyrola leaves using uredinial inoculum, even though success was achieved with other rust fungi. Fraser (1911, 1912, 1925) made a series of phenological observations and inoculation studies of the rust in Nova Scotia and Saskatchewan, Canada. He observed that uredinia on pyrola matured and began releasing spores by early May, and telia germinated in late May. Pistillate cones were opening on spruce in the vicinity. In early July, the pycnial state was evident with a yellowing of cone scales and a yellow-colored resin flow. Several controlled field and laboratory inoculation tests indicated that about 48 hours of moist environment was sufficient for infection of cones, although the number of infected cones was low.

Environmental requirements for infection of pyrola from urediniospores and aeciospores are probably more frequently met than for spruce cones from basidiospores because of the differing microenvironment of the host organs. Pyrola inhabits moist sites in the shade of dense tree stands, compared to the exposed tops of spruce trees. This difference would be greater in semiarid regions of the West, and perhaps less so in the Pacific Northwest.

Many species of *Pyrola* and two species of *Moneses* are known hosts of *C. pirolata* (Arthur 1934, Brown 1956, Shaw 1973). Damage to these species by the disease is apparently minor, with some atrophy and yellowing of leaves (Rice 1927, 1935). Disease symptoms reported on spruce cones in Canada include an early yellowing of cone scales, resin flow, premature browning, and—following aecial formation—a premature opening of the cones (Fraser 1912, Ziller 1974). Distortion or atrophy of cones is not indicated in the literature. Except for *Picea breweriana* S. Wats., *Picea chihuahuana* Martínez, and *Picea mexicana* Martínez, all native North American spruce species are known hosts of *C. pirolata* (Arthur and Kern 1906, Ziller 1957, Can. Dept. Environ. 1951–1975). Hedgcock (1912) described infected cones of Engelmann spruce (*Picea engelmannii* Parry) as aborted, with the only apparent damage being a reduction in seed crop. The infection is thought to spread completely throughout the cone (Savile 1950). Damage to seeds in rusted cones apparently can be severe. Rhoads et al. (1918) indicate that no seeds are produced in infected cones. In the United States (Zasada and Gregory 1969) and in Canada (Can. Dept. Environ. 1951–1975), reports indicate that no sound seeds are produced, although no germination studies were reported to support this. Eide (1927) in Norway found that 33 percent of the seeds from rusted cones germinated compared to 56.5 percent from nonrusted cones. Neger (1924) described diseased cones as forming little or no seed. In British Columbia, Sutherland (1981) found that the effect of cone rust on *Picea glauca* (Moench) Voss seed was to reduce yield, weight, and in some cases, the germinative capacity.

Sporadic, relatively localized epidemics appear to characterize the occurrence of *C. pirolata* spruce cone rust in the contiguous western United States. In contrast, in Alaska, Zasada and Gregory (1969) reported the rust on white spruce over an extensive area south of the Alaska range in 1960, and again in 1968 north of the Alaska range near Fairbanks. Ziller (1974) attributes an "A" damage rating ("causes great or significant damage") to inland spruce cone rust (caused by *C. pirolata*) in Canada. Damage ranging from light to nearly the entire cone crop destroyed in certain localities is reported regularly in the various provinces of Canada (Can. Dept. Environ. 1951–1975). Similar severity of damage occurs in Norway (Jørstad 1935, 1940; Roll-Hansen 1967).

Materials and Methods

Occurrence and habitat.— Our study was made in Huntington Canyon in central Utah in the area where a severe spruce cone rust epidemic occurred in 1969. During mid-September of that year, plots of about 0.1 ha were located at 1.6 km intervals along a 29 km length of the canyon. Sampling was limited to Colorado blue spruce in the riparian zone along Huntington Creek. The elevation, associated tree species, and presence of *Pyrola* spp. were noted at each interval. Number of spruce trees and number of spruce trees with cones were recorded for each plot. Five cone-bearing trees in each plot were examined closely for rusted cones. Rusted cones in the tops of trees were detected by using binoculars and, when in doubt, impacting the cone-bearing zone of the tree with shot from a 16-gauge shotgun. During the ensuing nine years, the area of the 1969 epidemic was checked annually in the fall for recurrence of the rust on spruce cones.

Phenological observations.— Information on the phenology of spruce cones and the rust fungus on pyrola was obtained by observing their development at about two-week intervals during spring and summer 1972. The plots were revisited for the cone observations, and one plot was established at the confluence on Left Fork and Huntington Creek for observation of the rust on *Pyrola* spp.

Observations of cone development were (1) emergence and/or elongation of ovulate cones from buds, (2) opening of ovulate cone scales during pollination, and (3) closing of cone scales following pollination. At each

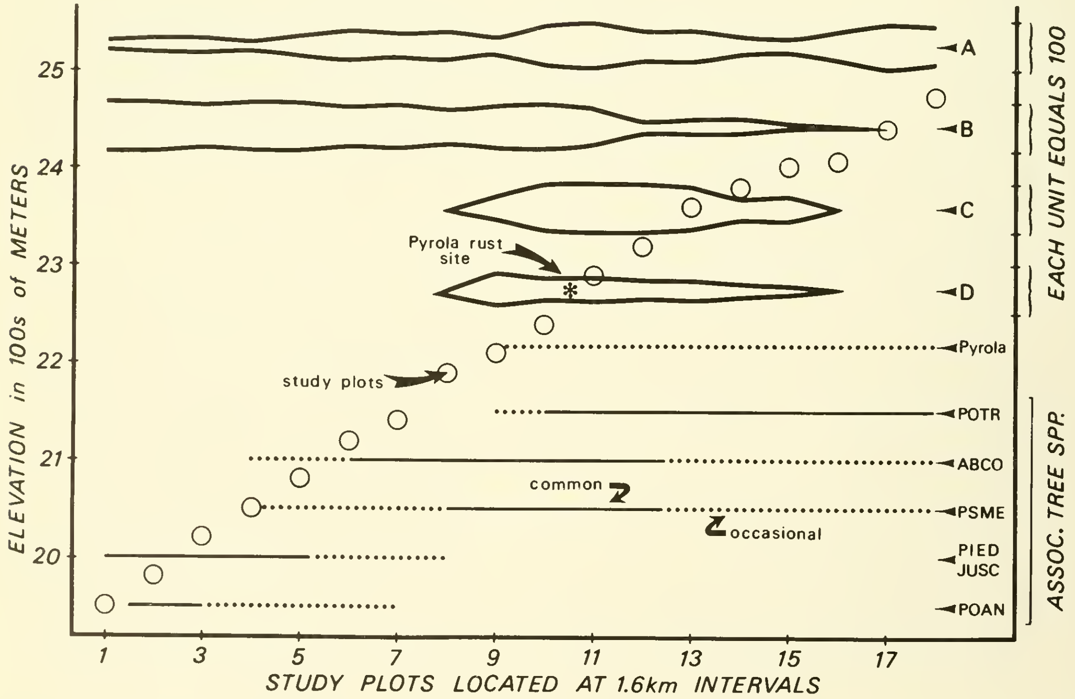


Fig. 1. Occurrence and habitat of *Chrysomyxa pirolata* in Huntington Canyon: A, Riparian Colorado blue spruce on study plots indicated as a percentage of the highest number found on plots; B, percentage of trees on study plots with ovulate cones of the current season; C, percentage of trees on study plots with rust infected cones; D, percentage of cones on study plots infected with rust. The prevalence of *Pyrola* and associated tree species is represented from estimates of plants in the immediate vicinity of study plots. *Pyrola* rust site, indicated by the asterisk, is the only site where the rust was found on *Pyrola*.

plot area, 5 to 10 trees were examined through binoculars. The record indicated "open" or "closed" when the majority of cones on trees were in either state. In the pyrola area, three sites were located within a half-kilometer; in each site several hundred *Pyrola asarifolia* Michx. plants were growing. At each observation, all rust-infected plants were examined for rust development. Observations were made for (1) emergence of uredinial-telial pustules, (2) rupture of the peridia, (3) dispersal of urediniospores, and (4) germination of teliospores.

Associated precipitation.— Weather data from an hourly recording station at Ephraim, Utah (about 38 km southwest of the site), were examined for precipitation during potential rust-infection periods in an effort to characterize the 1969 epidemic. We determined spring (May through June) and fall (mid-August through mid-October) precipitation totals and extended periods of rainy weather with 4–10 hours consecutive accumulation of 0.25 cm or more precipitation, and 10 or more hours with 0.13 cm or more precipitation. Some of the 4–10 hour periods had 1–2 hour gaps, and some of the 10 or more hour periods had 1–3 hour gaps in the hourly accumulation recording. A nonrecording rain gauge in Huntington Canyon at Stuart Guard Station, which was within the cone rust infection zone, yielded total summer (April through September) precipitation amounts. These were correlated with Ephraim records for 1956 through 1977 to form a basis .for projecting to Huntington Canyon the hourly precipitation data available at Ephraim.

Effect of spruce cone rust.— On plots with rusted cones, cone-bearing limbs were removed from one tree with a pole pruner to obtain 5 to 20 rusted and 5 to 20 nonrusted cone samples. The cones were placed in paper bags and dried in the laboratory for one month. Seed dispersal was simulated by tapping cones briskly on a table top; the remaining seeds were removed by breaking cones apart. "Dislodged" and "removed" seeds from rusted and nonrusted cones were kept separate for each plot. Seeds were prepared for germination tests by first washing under cold running tap water for 24 hours and then stratifying between moistened filter paper in Petri dishes. Stratification was for three months at 1 C. Germination tests were made by placing up to 100 randomly selected seeds per plot on moist filter paper in Petri dishes, and then incubating them under 15–25 C-day 15 C-night regime, using an 8-hour day at 1100 ft-c artificial lighting.

Results

Occurrence and habitat.— Huntington Canyon dissects southeasterly across the Wasatch Plateau of central Utah from an elevation of about 3000 m to Castle Valley 1300 m lower. In the lower reaches of the canyon,

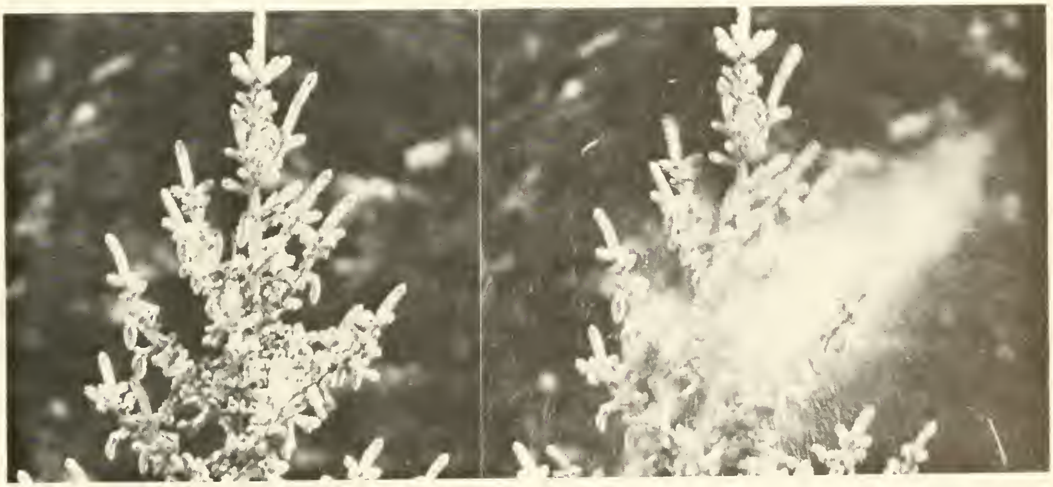


Fig. 2. Cone-bearing tip of Colorado blue spruce tree before shotgun blast (left) and cloud of cone rust spores at impact of shot (right).

the vertical displacement is about 900 m within a horizontal distance of 1–3 km. The canyon depth and northeasterly exposures provide typical coniferous habitat of the Intermountain West. In the lower, more arid portions of the canyon, riparian blue spruce was associated with pinyon-juniper (*Pinus edulis* Engelm.-*Juniperus scopulorum* Sarg.), narrow-leaf cottonwood (*Populus angustifolia* James), and scattered ponderosa pine (*Pinus ponderosa* Laws.). As elevation increased, Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco.) was present, and then the association changed primarily to white fir (*Abies concolor* [Gord. and Glend.] Lindl.), quaking aspen (*Populus tremuloides* Michx.), and an occasional Douglas-fir, Engelmann spruce, and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) in the upper canyon (Fig. 1). *Pyrola* spp. occurred on moist northerly exposures in dense spruce-fir stands in the central to upper portion of the canyon (Fig. 1). Both *Pyrola secunda* and *P. asarifolia* were present, the latter limited to springs and seeps. No pyrola was found within the pinyon-juniper zone.

Although cones were abundant on spruce, no rust was encountered for the first 13 km in the lower portion of the canyon. Cone rust was first encountered on Plot 9 at an elevation of 22 m (Fig. 1). For the next four plots, a distance of about 7 km, nearly 100 percent of the spruce trees were infected. Thereafter there was less infection until after Plot 15, at 2400 m; then none was observed, although cones were present on trees for another 1.6 km. The percentage of cones infected varied from 20–67 percent on the six plots where rust was encountered. The shotgun method of detection proved very effective in revealing presence of rusted cones in cases where initial detection with binoculars was questionable. Because our sampling was made during a prime time for aeciospore dispersal, large orange clouds of rust spores issued from the treetops upon impact of the shot (Fig. 2). The uredinial stage of the rust was found on *Pyrola secunda* and *P. asarifolia* in a spruce-fir stand midway between Plots 10 and 11 near the confluence of Left Fork and Huntington Creek. Although the canyon was not searched extensively, this was the only site

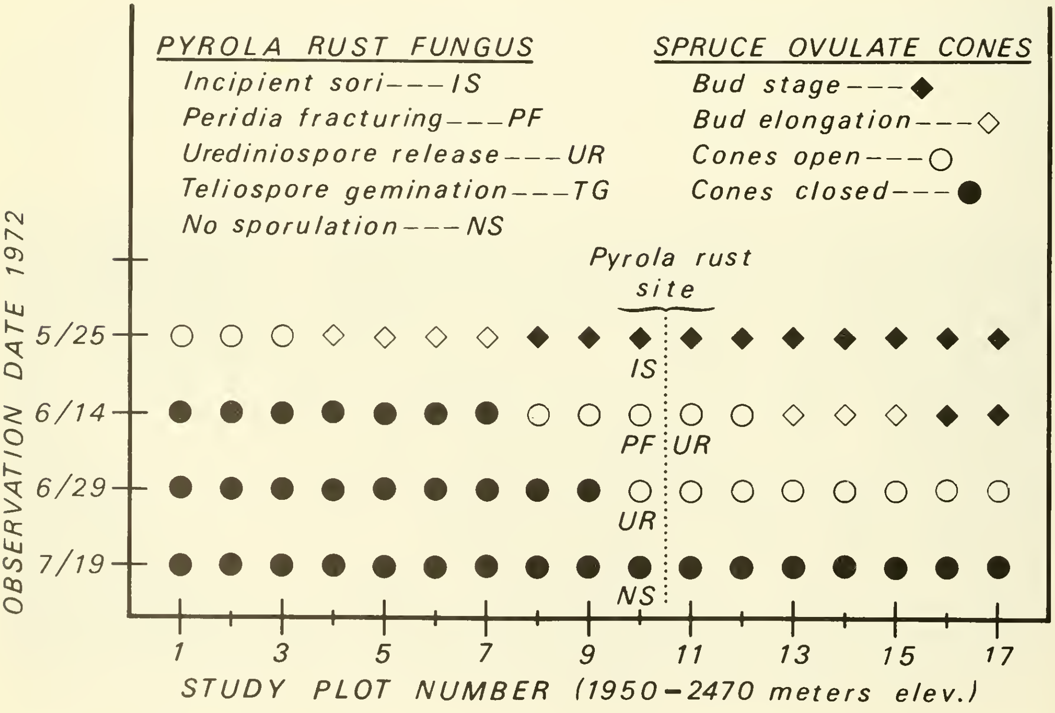


Fig. 3. Phenology of spruce ovulate cones and *Chrysomyxa pirolata* on *Pyrola* spp. in Huntington Canyon.

where the rust was found on pyrola. The annual checks from 1970 to 1978 of the area where the 1969 cone rust epidemic occurred failed to reveal the recurrence of any cone rust. Cones were present each year in varying amounts.

PHENOLOGY OF SPRUCE CONE RUST.— By 25 May of the year studied, ovulate cones were beginning to open at the lowest elevations of Huntington Canyon, but the strobilate buds were still dormant at 2200 m and above, throughout the pyrola zone (Fig. 3). Incipient uredinial-telial sori were visible on the lower leaf surfaces of pyrola near Plot 10. By 14 June, cones had opened and then closed to the 2100 m level and were open from 2200 m to 2300 m in the lower pyrola zone. A few uredinial peridia were rupturing with some spore dispersal in progress. Telia were present at the base of sori, but there was no evidence of germination. By 29 June, cones had closed at only slightly higher elevation, and cones were open throughout the upper canyon. Urediniospore dispersal was at a peak; teliospore formation was very sparse, and there was no evidence of germination. By 15 July, all spruce cones were long closed to the highest plot. Pyrola leaves with rust sori had dried up, and there was no evidence of telial germination.

Ovulate cones opened and closed within 20 days in the lower canyon. Sporulation of uredinial-telial sori lasted for 15–20 days beginning in mid-June. In 1969, aeciospore dispersal lasted from late August to at least through September.

ASSOCIATED PRECIPITATION.— A comparison of the yearly summer rainfall at Ephraim and Huntington canyons (Fig. 4) revealed a close correlation in annual fluctuations (correlation coefficient [r = 0.82]). The mean annual summer rainfall at Ephraim was 12.4 cm compared to 24.8 cm at Huntington Canyon, with similar deviations from the mean. During the 6 years preceding 1969 (the only year of known spruce cone rust outbreak), the annual precipitation at the Huntington Canyon site was above or near the 22-year mean, with no extreme years on the low side (Fig. 4). Following 1969, there was a downtrend with some near-mean years, but most were below the mean. The frequency of extended spring and fall rainy periods and precipitation totals at

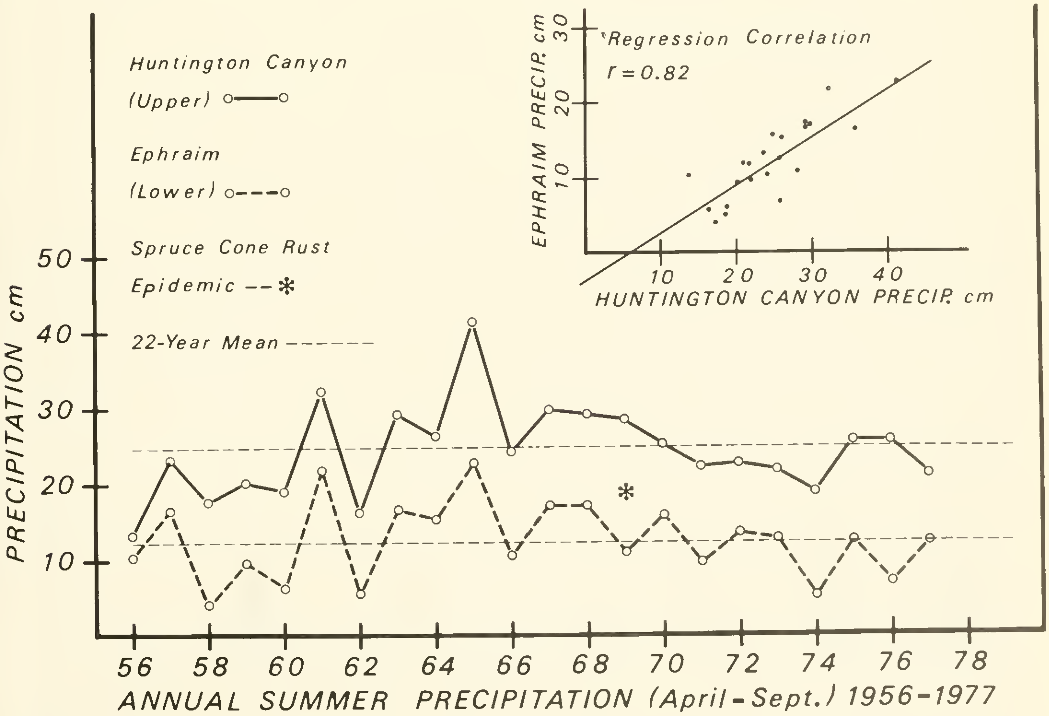


Fig. 4. Comparison of summer rainfall at Ephraim and Huntington canyons from 1956 through 1977.

Ephraim follow a similar pattern (Fig. 5). A continuity of extended periods of rainy weather during spring and fall occurred at Ephraim during the 4 years preceding 1969 that did not occur in the following 8 years. Years with similar extended rainy periods following 1969 (1970, 1972, 1973, 1975) were interrupted by dry seasons.

Effect of spruce cone rust.— Our observations of *Chrysomyxa pirolata* cone-rust symptoms were limited to mid-September, when aecia were well open. Depressed resinous areas were common on infected cones, usually on one side. The resinous areas appeared to have developed more slowly or incompletely, resulting in a slight twisting of the cone. Cone scales opened prematurely on rusted compared to nonrusted cones, and were often twisted and malformed (Fig. 6). Not all infected cones appeared to be completely infected; or at least in some parts of the cone, no aecial development occurred, and cone scales did not open prematurely. These areas were usually on the upper portion of cones (Fig. 7). Aecia formed primarily in a zone peripheral to the seeds (Fig. 8).

An evaluation (Table 1) revealed that nonrusted cones yielded an average of 204 apparently sound seeds, and rusted cones 188. Seeds likely to disperse readily averaged 113 for nonrusted and 13 for rusted. A check of overwintered cones (12 nonrusted, 9 rusted) at the Huntington Canyon site the following summer showed an average of 18 seeds per cone remaining in nonrusted cones and 86 in rusted cones. Viability of seeds extracted from cones as determined by germination tests is indicated in Table 2. Of seeds dislodged by tapping cones, 71.0 percent germinated from nonrusted cones compared to 48.9 percent from rusted cones. Remaining seed extracted by breaking cones apart germinated at 53.3 percent for nonrusted and 34.8 percent for rusted.

Discussion and Conclusions

Occurrence, habitat, and phenology.— In Huntington Canyon located in central Utah's high plateau country, *Chrysomyxa pirolata* cone rust of blue spruce was observed in a rare epidemic phase. Cone rust

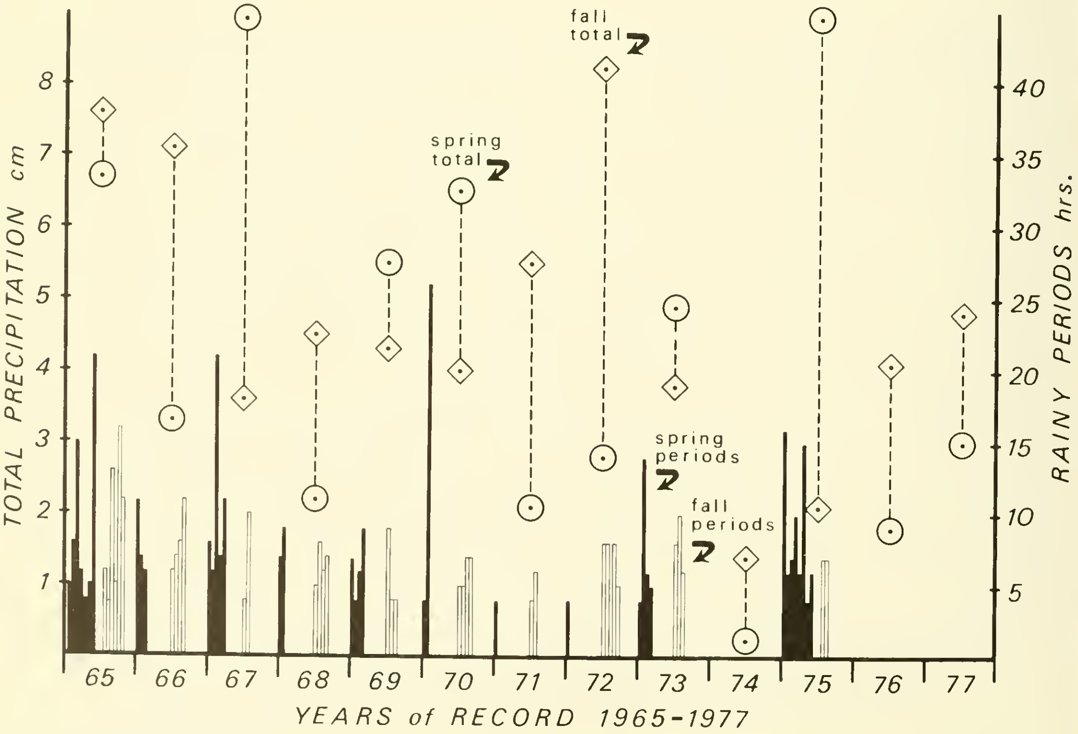


Fig. 5. Extended hourly rainy periods and spring and fall precipitation at Ephraim, Utah.

was limited to the spruce-fir zone where *Pyrola* spp. also occurred. Riparian blue spruce extended to lower elevations in the pinyon-juniper zone where neither cone infection nor pyrola were found. Cones were present on spruce above and below the cone rust zone. Studies by Fraser (1911, 1912, 1925) indicate that pistillate cones are susceptible to infection when cone scales open for pollination; however, the precise period of susceptibility has not been established. In our study, the period of cone opening observed was closely correlated with the onset of uredinial-telial sporulation. During the single season observed, cones at lower elevations opened and closed 20 days or less prior to when the rust fungus began sporulation. Phenological progress in cone development with elevation, it appears, could limit the distance of infection from a point inoculum source. In Norway (Roll-Hansen 1967), the greatest incidence of cone rust was found at higher elevations and more northern latitudes; however, abundant infection of pyrola occurred elsewhere. The cause was attributed to unfavorable climatic conditions for infection of spruce cones in these areas. *Chrysomyxa pirolata* cone rust is rare in Canadian Pacific Coast areas compared to other parts of western Canada (Ziller 1974). Climate and telial hosts did not appear to be limiting since the closely related *Chrysomyxa monesis* Ziller occurs on Sitka spruce (*Picea sitchensis* [Bong.] Carr.) cones and *Moneses uniflora* (L.) A. Gray in coastal areas (Ziller 1974). Our study did not include investigation of variation in duration of favorable moisture during precipitation periods with elevation. However, evidence suggests that host phenology as well as habitat as influenced by elevation is a factor in the progressively narrower niches of the spruce cone-rust fungus proceeding southward across the continent from northern latitudes. The uredinial-telial sporulation period lasted for 15–20 days, beginning in mid-June. The 1972 spring season was later than normal, and therefore spore dispersal could occur from May through June into early July. Teliospores did not develop fully, and there was no germination evident. This result was likely because of the dry spring of 1972 (Figs. 4 and 5). This also may have speeded the death of pyrola leaves upon which sori formed. Fraser (1911), in eastern Canada, and Rice (1927), in the New England states, observed that teliospore formation followed urediniospore formation by several weeks. Although there was poor telial formation in our study, it appeared to be almost simultaneous with uredinial formation as Savile (1950) reported, and is typical of the *Chrysomyxa* rust fungi in general (Ziller 1974). Periods of rainy weather may be necessary for abundant teliospore formation.

Even though the aecial-pycnial stage on spruce is apparently relatively rare in the southern distribution of this cone rust on the North American Continent, it is significant that the sexual stage does occur. There is then the chance for genetic recombination and diversification of the rust fungus without dependence on migration of genes from northern latitudes on *Pyrola*.

Associated precipitation.— The close correlation of Huntington Canyon and Ephraim summer precipitation fluctuations allowed some confidence in projecting the Ephraim hourly record. Other than elevation, most differences are probably accounted for by short-term thunderstorms. Duration of extended rain at Huntington Canyon, however, was likely longer because the total precipitation was nearly twice the amount at Ephraim. Rainy periods of four hours or more in spring and fall were infrequent in the 13-year-record studied (Fig. 5), and therefore the

Table 1. Effect of *Chrysomyxa pirolata* cone rust on blue spruce seed yield and dispersal.

		Average no. seeds per cone		
	No. cones[1]	Dislodged by tapping	Removed by breaking	Total
Nonrusted	89	113	91	204
Rusted	48	13	175	188

[1]Total cones from six plots.

Table 2. Effect of *Chrysomyxa pirolata* cone rust on viability of blue spruce seed.

	No. seeds[1]		% Germination	
	Nonrusted	Rusted	Nonrusted	Rusted
Dislodged by tapping	600	325	71.0	48.9
Removed by breaking	600	600	53.3	34.8

[1]Maximum 100 seeds per plot.

coincidence of susceptible cones, favorable moisture, and fungus inoculum is also probably infrequent. Based on spring rainy periods, the chance for favorable moisture for infection during springs of 1970, 1973, and 1975 appears just as positive as 1969, although no cone infection was detected.

Perhaps, then, a continuity of extended spring and fall rains over several years is necessary for an epidemic. With dry seasonal interruptions, the fungus population could decline to levels that do not permit detectable amounts of cone infection even though spring rains during some years may be favorable. There is, however, no cause-and-effect relationship established here. There is not enough reliable knowledge about the epidemiology of *C. pirolata* cone rust to relate epidemics to weather records in a precise sense.

The urediniospores produced on the *Pyrola* spp. observed in this study adhered rather strikingly, suggesting that dispersal may be primarily by rain splash, thus restricting intensification of the rust in the uredinial phase to the immediate locality. Widespread dispersal of the fungus to pyrola would then seem to be more dependent on aeciospores that are readily dislodged from cones over a long period. If these possibilities are true, it would lend support to the importance of fall rainy periods. Because of the systemic-perennial nature of the pyrola rust infection, an important factor in the need for consecutive years of favorable moisture would be the number of years rusted pyrola plants live.

Effect of spruce cone rust.— Symptoms of *C. pirolata* cone rust of Colorado blue spruce observed in this study were somewhat different from what is reported in the literature for other species of spruce. Depressed resinous areas on infected cones appeared to cause slight twisting of the cones. Portions of infected cones appeared to be rust free, or at least there were areas where no aecia formed. Aecial pustules formed primarily in a zone peripheral to the seeds, which may be related to the amount of seed damage. The disease appeared to have only a slight effect on development of seeds. There was about a 25 percent reduction in seed germinability with seed from rusted cones. This indicates that cone rust of blue spruce is less damaging to seed development than reported for other species of spruce. Relatively few seeds could

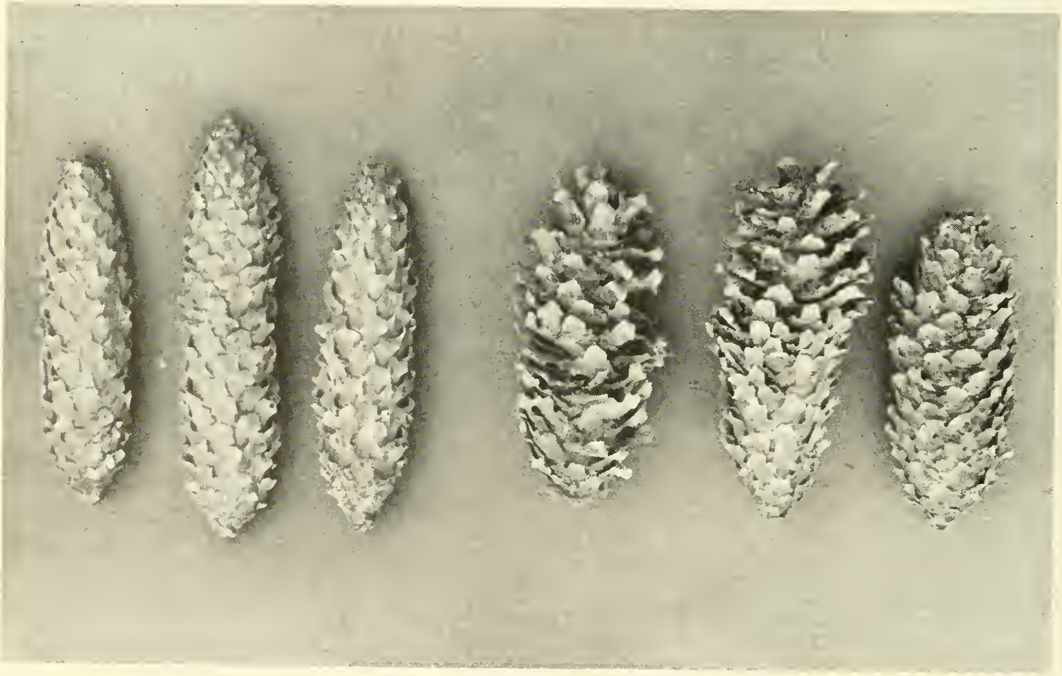


Fig. 6. *Chrysomyxa pirolata* rust-diseased Colorado blue spruce cones (three left) and nonrusted cones (three right). Note the twisted, malformed nature of the rusted compared to nonrusted cones.

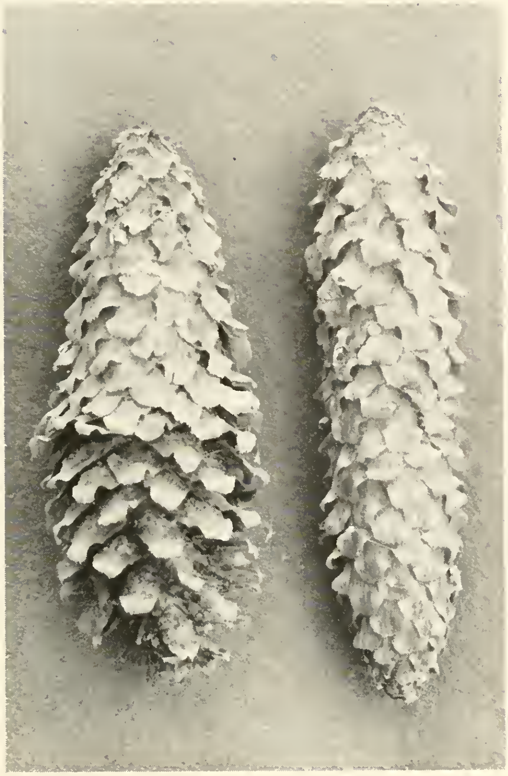


Fig. 7. Rusted (left) and nonrusted (right) cones of blue spruce. Note that cone scales on upper half of rusted cone have not opened.

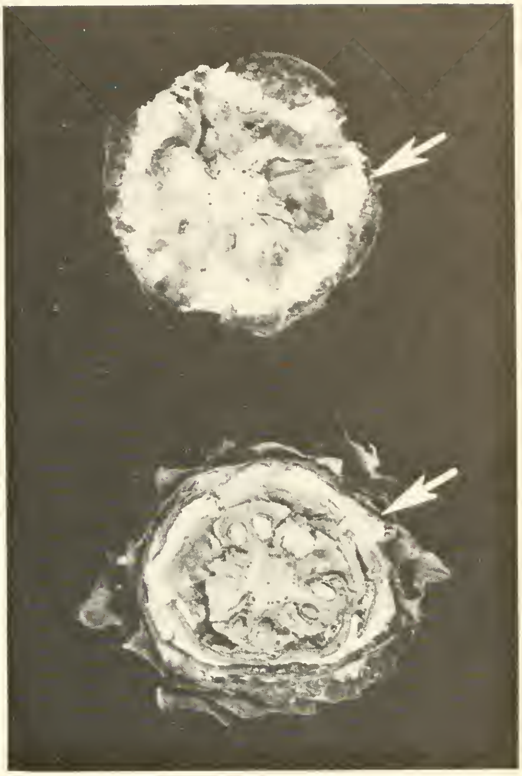


Fig. 8. Rust-infected blue spruce cones in cross section. Note that "white" spore masses are peripheral to the inner seed zone.

be easily dislodged artificially from rusted cones compared to nonrusted. This indicates that the disease severely impedes seed dispersal; and this was substantiated upon examination of naturally overwintered cones. Aecial spore masses, resinosus, and malformation of cone scales prevented seed dispersal to the extent that the seed crop was effectually destroyed.

Literature Cited

Arthur, J. C. 1907–1931. Order Uredinales. Pages 1–969 *in* North America Flora. Vol. 7, Part 2–13. New York Botanical Gardens, New York.

_____. 1934. Manual of the rusts in the United States and Canada. Purdue Research Foundation, Lafayette, Indiana. 438 pp.

Arthur, J. C., and F. D. Kern. 1906. North American species of *Peridermium*. Bull. Torrey Bot. Club 33:403–438.

Brown, A. M. 1956. A checklist of plant rusts in Canada. Canada Dept. of Agric. Publ. 976. 51 pp.

Canada Department of Environment. 1951–1975. Annual Report, Forest Insect and Disease Survey, Canadian For. Serv., Queen's Printer, Ottawa.

Cash, E. K. 1953. A checklist of Alaskan fungi. Plant Dis. Reptr. Suppl. 219. 70 pp.

Clinton, G. R., and F. A. McCormick. 1919. Rust infection on leaves in Petri dishes. Conn. Agric. Expt. Sta. Bull. 260:475–501.

Cummins, G. B. 1943. Annotated checklist and host index of the rusts of Guatemala. Plant Dis. Reptr. Suppl. 142. 131 pp.

Eide, E. 1927. Undersøkelse av nordenfjelsk granfrø 1925. Med. fra Det Norske Skogforsøksvesen, H. 8:15–39.

Fraser, W. P. 1911. Cultures of some heteroecious rusts. Mycologia 3:67–74.

_____. 1912. Cultures of heteroecious rusts. Mycologia 4:175–193.

_____. 1925. Culture experiments with heteroecious rusts in 1922, 1923, and 1924. Mycologia 17:78–86.

Gäumann, E. 1959. Die Rostpilze Mitteleuropas, Bulcher Co., Bern. Beitrage zur Kryptogamenflora der Schweiz, Bd. 12.

Gilbertson, R. L., and J. McHenry. 1969. Checklist and host index for Arizona rust fungi. Univ. of Ariz. Agric. Expt. Sta. Tech. Bull. 186. 40 pp.

Hedgcock, G. G. 1912. Notes on some western Uredineae which attack forest trees. Mycologia 4:141–147.

Jørstad, I. 1935. Uredinales and Ustilaginales of Trøndelag. Det Kyl Norske Videnskabers Selskabs Skrifler NR 38. 90 pp.

———. 1940. Uredinales of northern Norway. Skr. utg. av. Det. Norske Vindensk.-Akad. i, Oslo. I. Mat.-Naturv. Klasse. 1940. No. 6. 145 pp.

Kimmey, J. W., and J. A. Stevenson. 1957. A forest disease survey of Alaska. Plant Dis. Reptr. Suppl. 247. pp. 87–98.

Martínez, M. 1963. Las Pináceas Méxicanas, 3d ed. Universidad Nacional Autónoma de México, México City. 401 pp.

Neger, F. W. 1924. Die krankheiten unserer Waldbäume und der wichtigsten Gartengehölze. 2d ed. Ferdinand Enke, Stuttgart. 296 pp.

Nelson, D. L., and R. G. Krebill. 1970. Effect of *Chrysomyxa pirolata* cone rust on dispersal and viability of *Picea pungens* seeds. Phytopathology Abstr. 60:1305.

Peterson, R. S. 1961. Notes on western rust fungi. I. *Chrysomyxa*. Mycologia 53:427–431.

Rhoads, A. S., G. G. Hedgcock, E. Bethel, and C. Hartley. 1918. Host relationships of the North American rusts other than Gymnosporangiums, which attack conifers. Phytopathology 8:309–352.

Rice, M. A. 1927. The haustoria of certain rusts and the relation between host and pathogen. Bull. Torrey Bot. Club 54:63–153.

———. 1935. The cytology of host-parasite relations. Bot. Rev. 1:327–354.

Roll-Hansen, F. 1967. On diseases and pathogens of forest trees in Norway, 1960–1965. (Om sykdommer og patogener på skograernei Norge, 1960–1965). Saertrykk av Meddelelser fra Det Norske Skogforsøksvesen. Vollebekk, Norge. Nr. 80, Bind XXI, pp. 174–246.

Savile, D. B. O. 1950. North American species of *Chrysomyxa*. Canadian Jour. Resc. 28:318–330.

———. 1953. Short-season adaptations in the rust fungi. Mycologia 45:75–87.

Shaw, C. G. 1973. Host fungus index for the Pacific Northwest—I. Hosts;—II. Fungi. Washington Agric. Expt. Sta. Bull. 765, 766.

Sutherland, J. R. 1981. Effects of inland spruce cone rust, *Chrysomyxa pirolata* Wint., on seed yield, weight and germination. Canadian For. Serv., Res. Notes 1(2):8–9.

Zasada, J. C., and R. A. Gregory. 1969. Regeneration of white spruce with reference to interior Alaska: a literature review. USDA For. Serv. Res. Pap. PNW-79, 37 pp.

Ziller, W. G. 1957. Fungi of British Columbia deposited in the herbarium of the Forest Biology Laboratory, Victoria, BC, Canada. For. Biol. Div., Sci. Serv., Agric. Dept., Ottawa, Canada.

———. 1974. The tree rusts of western Canada. Canada Dept. Environ., Canadian For. Serv. Publ. No. 1329. 272 pp.

NOTICE TO CONTRIBUTORS

Manuscripts intended for publication in the *Great Basin Naturalist* or *Great Basin Naturalist Memoirs* must meet the criteria outlined in paragraph one on the inside front cover. They should be directed to Brigham Young University, Stephen L. Wood, Editor, Great Basin Naturalist, 290 Life Science Museum, Provo, Utah 84602. Three copies of the manuscript are required. They should be typewritten, double spaced throughout on one side of the paper, with margins of at least one inch on all sides. Use a recent issue of either journal as a format, and the *Council of Biology Editors Style Manual, Fourth Edition* (AIBS 1978) in preparing the manuscript. An abstract, about 3 percent as long as the text, but not exceeding 200 words, written in accordance with *Biological Abstracts* guidelines, should precede the introductory paragraph of each article.

All manuscripts receive a critical peer review by specialists in the subject area of the manuscript under consideration. Authors may recommend one or two reviewers for their article.

Accepted manuscripts less than 100 printed pages in length will automatically be assigned to the *Great Basin Naturalist*. Those larger than 100 printed pages will be considered for the *Memoirs* series.

Illustrations and Tables. All illustrations and tables should be made with a view toward having them appear within the limits of the printed page. The original illustrations or glossy photoprints of them should accompany the manuscript. Illustrations should be prepared for reduction by the printer to either single-column (2⅝ inches) or double-column (5½ inches) width, with the length not exceeding 7½ inches.

Costs Borne by Contributor. Contributors to the *Great Basin Naturalist* should be prepared to donate from $10 to $40 per printed page toward publication of their article (in addition to reprint costs). Excessive or complex tables requiring typesetting may be charged to the author at cost. Authors publishing in the *Great Basin Naturalist Memoirs* may be expected to contribute $40 per printed page in addition to the cost of the printed copies they purchase. No reprints are furnished free of charge.

Reprint Schedule for the *Great Basin Naturalist*

100 copies, minimum cost for 2 pages, $26.
Each additional 2 pages, $6.
Each additional 100 copies, $4 for each 2 pages.
Examples: 300 copies of 10 pages = $82; 200 copies of 13 pages = $86.

Great Basin Naturalist Memoirs

No. 1	The birds of Utah. By C. L. Hayward, C. Cottam, A. M. Woodbury, H. H. Frost. $10.
No. 2	Intermountain biogeography: a symposium. By K. T. Harper, J. L. Reveal et al. $15.
No. 3	The endangered species: a symposium. $6.
No. 4	Soil-plant-animal relationships bearing on revegetation and land reclamation in Nevada deserts. $6.
No. 5	Utah Lake monograph. $8.
No. 6	The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. $60.

TABLE OF CONTENTS

Utah plant types—historical perspective 1840 to 1981—annotated list, and bibliography. Stanley L. Welsh 129

A new species of *Cryptantha* (Boraginaceae) from Nevada. Kaye H. Thorne and Larry C. Higgins 196

New taxa of thistles (*Cirsium*: Asteraceae) in Utah. Stanley L. Welsh 199

A species of *Cryptantha* (Boraginaceae) dedicated to the memory of F. Creutzfeldt. Stanley L. Welsh 203

Algal populations in Bottle Hollow Reservoir, Duchesne County, Utah. Jeffrey Johansen, Samuel R. Rushforth, and Irena Kaczmarska 205

Herpetological notes from the Nevada Test Site. Wilmer W. Tanner 219

New species of American bark beetles (Coleoptera: Scolytidae). Stephen L. Wood 223

Temperature-related behavior of some migrant birds in the desert. George T. Austin and J. Scott Miller 232

Description of a new *Phalacropsylla* and notes on *P. allos* (Siphonaptera: Hystrichopsyllidae). R. B. Eads and E. G. Campos 241

Vegetation of the mima mounds of Kalsow Prairie, Iowa. Jack D. Brotherson 246

Occurrence and effect of *Chrysomyxa pirolata* cone rest on *Picea pungens* in Utah. David L. Nelson and Richard G. Krebill 262

THE GREAT BASIN NATURALIST

Volume 42 No. 3 September 30, 1982 Brigham Young University

MUS. COMP. ZOOL
LIBRARY
FEB - 2 1983
HARVARD
UNIVERSITY

GREAT BASIN NATURALIST

Editor. Stephen L. Wood, Department of Zoology, 290 Life Science Museum, Brigham Young University, Provo, Utah 84602.

Editorial Board. Kimball T. Harper, Chairman, Botany; James R. Barnes, Zoology; Hal L. Black, Zoology; Stanley L. Welsh, Botany; Clayton M. White, Zoology. All are at Brigham Young University, Provo, Utah 84602.

Ex Officio Editorial Board Members. Bruce N. Smith, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications.

Subject Area Associate Editors.

Dr. Noel H. Holmgren, New York Botanical Garden, Bronx, New York 10458 (Plant Taxonomy).

Dr. James A. MacMahon, Utah State University, Department of Biology, UMC 53, Logan, Utah 84322 (Vertebrate Zoology).

Dr. G. Wayne Minshall, Department of Biology, Idaho State University, Pocatello, Idaho 83201 (Aquatic Biology).

Dr. Ned K. Johnson, Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720 (Ornithology).

Dr. E. Philip Pister, Associate Fishery Biologist, California Department of Fish and Game, 407 West Line Street, Bishop, California 93514 (Fish Biology).

Dr. Wayne N. Mathis, Chairman, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 (Entomology).

Dr. Theodore W. Weaver III, Department of Botany, Montana State University, Bozeman, Montana 59715 (Plant Ecology).

The *Great Basin Naturalist* was founded in 1939 and has been published from one to four times a year since then by Brigham Young University. Previously unpublished manuscripts in English of less than 100 printed pages in length and pertaining to the biological natural history of western North America are accepted. Western North America is considered to be west of the Mississippi River from Alaska to Panama. The *Great Basin Naturalist Memoirs* was established in 1976 for scholarly works in biological natural history longer than can be accommodated in the parent publication. The *Memoirs* appears irregularly and bears no geographical restriction in subject matter. Manuscripts are subject to the approval of the editor.

Subscriptions. The annual subscription to the *Great Basin Naturalist* for private individuals is $16.00; for institutions, $24.00 (outside the United States, $18.00 and $26.00); and for student subscriptions, $10.00. The price of single issues is $6.00 each. All back issues are in print and are available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to Brigham Young University, *Great Basin Naturalist,* 290 Life Science Museum, Provo, Utah 84602. The *Great Basin Naturalist Memoirs* may be purchased from the same office at the rate indicated on the inside of the back cover of either journal.

Scholarly Exchanges. Libraries or other organizations interested in obtaining either journal through a continuing exchange of scholarly publications should contact the Brigham Young University Exchange Librarian, Harold B. Lee Library, Provo, Utah 84602.

Manuscripts. See *Notice to Contributors* on the inside back cover.

11-82 650 61360

ISSN 017-3614

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 42 September 30, 1982 No. 3

BUCCAL FLOOR OF REPTILES, A SUMMARY

Wilmer W. Tanner[1] and David F. Avery[2]

ABSTRACT.— A general survey of the information presently available on the osteology and myology of the hyobranchial apparatus. Included in the survey are examples of the hyobranchial skeleton of the major groups of reptiles, including the Chelonia, Crocodilia, Rhynchocephalia, and Squamata. The myology treats the muscles directly associated with the hyoid as well as those associated with the functioning of the apparatus, but not arising or inserted directly on or from the hyoid. The innervation of the hyobranchial apparatus is reviewed and briefly discussed based on the information available in a few major studies. An attempt is made to cite all pertinent literature references, and in Tables 1 and 2 the references to basic areas are indicated. Twenty-nine plates and figures are included, some of which represent original research.

I. INTRODUCTION

Few anatomical areas have been subjected to such pronounced evolutionary changes as have the branchial apparatus and its derivatives in the vertebrate series. The hyoid apparatus has responded to these numerous adaptive changes with structural and functional modifications. One needs only to contemplate the change necessary in adapting from a structure bearing gills to one associated with lungs, from an immovable to a highly flexible tongue, or to the development of a larnyx and archaic voice to appreciate the anatomical importance of this area. Furthermore, the class Reptilia consists of both primitive (turtles, crocodilians, and *Sphenodon*) and specialized (lizards and snakes) forms that include organisms possessing considerable structural diversification.

In reptiles the buccal floor consists of osseous and cartilaginous elements of the branchial skeleton and the associated connective and muscular tissues. Included among the skeletal elements are the jaws, hyoid apparatus, laryngeal cartilages, and tracheal rings. The associated fleshy parts include the hypobranchial throat musculature, the tongue, and the nerves and blood vessels associated with them. There is also a variety of glands associated with the buccal floor; these are usually involved with the production of saliva that may be poisonous.

A complete comparative anatomical treatise on the buccal floor is not possible at this time, primarily because the necessary information is not available. Some anatomical studies on reptiles are precise and show considerable detail; however, the studies have too often been concerned primarily with one series of bones or one group of muscles rather than an entire anatomical pattern. As a result, we will confine our remarks to the present knowledge of the hyoid structure and associated muscles and nerves in the floor of the reptilian mouth. Many studies touch on the subject at hand in various ways. We have, therefore, included in the bibliography many studies not cited in the text. These have been useful in our examination of the materials available and are as follows: Adams 1919, 1925, Ashley 1955, Barrows and Smith 1947, Beddard 1905, Bellairs 1950, Bergman 1961, 1965, Boltt and Ewer 1964, Brock 1938, Bullock and Tanner 1966, Byerly 1926, Chaine 1902, Chiasson 1962, Cowan and Hick 1951, Davis 1934, Duda 1965, Dullemeijer 1956, 1958, El Toubi 1938, 1947a, 1947b, El Toubi and Kalil 1952, Eyal-Giladi 1964, Evans 1955, Gandolfi 1908, Gans 1961, George 1948, George and Shad 1954, 1955, Haas 1952, 1960, 1968, 1973, Harris 1963, Heymans 1970, Iordansky 1970, Iyer 1942, 1943, Kamal, Hammouda, and Mokhtar 1970, Kesteven 1944, Kingman 1932, Kluge 1962, Kochva 1958, Liem, Marx, and Rabb 1971, Mahendra 1949, Malam 1941, McKay 1889, Minot 1880, Mivart 1867, Norris and Lowe 1951, Oldham, Smith, and Miller 1970, Parker 1880, Ping 1932, Presch 1971, Rathor 1969, Reese 1923, Rice 1920, Rieppel 1981, Rosenberg 1968, Sanders 1870, 1872, 1874, Schumacher 1956c, Sewertzoff 1929, Shah 1963, Sidky 1967, Siebenrock 1892a, 1892b, 1893, 1894, 1895, Sinitsin 1928, and Varkey 1979.

---

[1] Life Science Museum, Brigham Young University, Provo, Utah 84602.

[2] Department of Biology, Southern Connecticut State College, New Haven, Connecticut 06515.

Tables 1 and 2 provide additional information on the material covered by these and other authors dealing with buccal floor and associated structures.

II. Hyoid Apparatus

General

The branchial skeleton, including the visceral arches, which we have associated with the more primitive gill-bearing vertebrates, has been recast in the tetrapods where its structure and function have been modified. The branchial skeleton now appears in tetrapods as a part of the skull; it includes the jaw and the hearing apparatus, as well as the larynx and trachial cartilage supports. The tetrapod has also retained the more central part of the old visceral skeleton, which is now known as the hyoid apparatus.

Because reptiles have lost the gill apparatus in all stages of development, the hyoid apparatus has assumed the function of a support for the tongue, glottis, and sometimes an extended dewlap. In modern reptiles, the hyoid is composed of several osseous and cartilagenous elements and exhibits a variety of degrees of ossification. As a general rule, the larger (or older) the animal, the more ossified is the hyoid apparatus. In most reptiles, except in some snakes, the hyoid apparatus is a spreading, flexible structure that occupies space in, and forms a support for, most of the floor of the oropharynx.

Although the phylogenetic relationships of the hyoid apparatus and visceral arches are not completely understood, it is known that the hyoid apparatus is derived from the hyoid cartilage and the two succeeding arches. Romer (1956) believes that the hyoid of ancestral reptiles must have been more extensive and that traces of a third branchial cornu can be seen in some reptilian embryos. The third cornu is well demonstrated in monotreme mammals.

The nomenclature pertaining to the hyoid is not uniform. Furbringer (1922) describes the first two pairs of arches as the cornu hyale and the cornu brachiale I, respectively; the third arch is called the cornu branchiale II. This latter arch is referred to by Beddard (1907) as the branchial process and as the basibranchial by Gnanamuthu (1937). The third arch is seemingly absent in several reptiles, causing some workers to refer to the remaining two arches as the anterior and posterior cornua. Unfortunately, the identity of the third arch has not been clearly ascertained. The third arch may be a degenerate structure expressed as projections from the basihyoid or body of the hyoid, or it may be present as a separate arch with either the first or second arch being lost. In the Ophidia and some burrowing lizards such as *Anniella*, *Dibamus*, *Acontias*, *Acontophiops*, and *Typhlosaurus*, the hyoid is greatly reduced and the identity of the posterior cornua is not positively established. (See Rieppel 1981 for a more complete discussion.) A similar situation exists in the Testudines and Crocodilia. The development of the hyoid apparatus has been discussed by Rathke (1839), Kallius (1901), Howes and Swinnerton (1901), Peyer (1912), Edgeworth (1935), DeBeer (1937), Pringle (1954), El Toubi and Kamal (1959a,b), El Toubi and Majid (1961), Kamal and Hammouda (1965), Langebartel (1968), Rieppel (1981), and others (Table 1). These

TABLE 1. Publications dealing with the buccal floor of reptiles.

Genus	Hyoid	Tongue	Musculature	Nerves
Order Chelonia **Suborder Pleurodina**				
Pelomedusidae				
Pelusios			Poglayen-Neuwall 1953	Poglayen-Neuwall 1953
Chelidae				
Batrochemys			Poglayen-Neuwall 1953	Poglayen-Neuwall 1953
Chelodina	Furbringer 1922	Winokur 1974	Graper 1932 Kesteren 1944 Poglayen-Neuwall 1953 Shah 1963	Kesteren 1944 Poglayen-Neuwall 1953
Suborder Cryptodira				
Dermatemydidae				
Dermatemys	Furbringer 1922			
Chelydridae				
Chelydra	Furbringer 1922 Edgeworth 1935 Schumacher 1973	Winokur 1974	Camp 1923 Graper 1932 Poglayen-Neuwall 1953 Schumacher 1973	Poglayen-Neuwall 1953 Soliman 1964
Kinosternon	Furbringer 1922 Schumacher 1973		Poglayen-Neuwall 1953 Schumacher 1973	Poglayen-Neuwall 1953
Sternotherus	Furbringer 1922 Schumacher 1973		Poglayen-Neuwall 1953 Schumacher 1973	Poglayen-Neuwall 1953
Testudinidae				
Chrysemys	Furbringer 1922 Ashley 1955 Schumacher 1973		Poglayen-Neuwall 1953 Ashley 1955 Schumacher 1973	Poglayen-Neuwall 1953
Clemmys	Siebenrock 1898 Furbringer 1922 Schumacher 1973		Graper 1932 Lubosch 1933 Schumacher 1973	Lubosch 1933 Poglayen-Neuwall 1953
Cuora	Furbringer 1922		Poglayen-Neuwall 1953	Poglayen-Neuwall 1953
Deirochelys			Shah 1963	
Dermatemys	Furbringer 1922	Winokur-Pers. Comm.		
Emys	Walter 1887 Furbringer 1922 Schumacher 1973	Sewentzoff 1929	Walter 1887 Schumacher 1973	Poglayen-Neuwall 1953
Gopherus		Winokur 1973	George & Shad 1955	

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Graptemys			Poglayen-Neuwall 1953	Poglayen-Neuwall 1953
Geochelone (*Testudo*)	Bojanus 1819 Furbringer 1922 Edgeworth 1935 Hacker & Schumacher 1955 Schumacher 1973	Bojanus 1819	Bojanus 1819 Graper 1932 Edgeworth 1935 Lubosch 1933 Poglayen-Neuwall 1953 Schumacher 1973	Lubosch 1933 Poglayen-Neuwall 1953
Malachemys			Poglayen-Neuwall 1953	Poglayen-Neuwall 1953
Pseudemys	Furbringer 1922 Schumacher 1973		Ashley 1955 Poglayen-Neuwall 1953 Schumacher 1973	Poglayen-Neuwall 1953
Terrapene	Furbringer 1922		Poglayen-Neuwall 1953	Poglayen-Neuwall 1953
Trionychidae				
Trionyx (*Amyda*)	Siebenrock 1898 Sondhi 1958 Furbringer 1922 Schumacher 1973	Sondhi 1958	Graper 1932 Lubosch 1933 Poglayen-Neuwall 1953 Schumacher 1973	Poglayen-Neuwall 1953
Lissemys	Furbringer 1922 Sondhi 1958 Schumacher 1973	Gnananuthu 1937 Sondhi 1958	George & Shad 1954 Sondhi 1958 Schumacher 1973	
Cheloniidae				
Caretta	Furbringer 1922 Schumacher 1973		Poglayen-Neuwall 1953 Schumacher 1973	Poglayen-Neuwall 1953
Dermachelyidae				
Dermochelys	Schumacher 1973		Poglayen-Neuwall 1953 Poglayen-Neuwall 1953/54 Schumacher 1973	Poglayen-Neuwall 1953 Poglayen-Neuwall 1953/54
Order Rhynchocephalia				
Sphenodontidae				
Sphenodon	Osawa 1898 Howes & Swinnerton 1901 Furbringer 1922 Edgeworth 1931,35 Rieppel 1978	Sewertzoff 1929	Osawa 1898 Camp 1923 Byerly 1926 Edgeworth 1931,35 Lightoller 1939 Kesteven 1944 Rieppel 1978	Osawa 1898 Lubosch 1933 Kesteven 1944 Rieppel 1978

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Order Squamata **Suborder Sauria**				
Gekkonidae				
Ascolabotes		Sewertzoff 1929	Camp 1923 Edgeworth 1935	
Cnemaspis	Richter 1933			
Coleonyx	Camp 1923 Kluge 1962		Camp 1923	
Eublepharis	Cope 1892 Camp 1923			
Gehrydra	Richter 1933			
Gekko	Camp 1923 Richter 1933		Camp 1923 Lubosch 1933	Lubosch 1933
Gymnodactylus	Richter 1933		Brock 1938 Kesteven 1944	Kesteven 1944
Hemidactylus	Zavattari 1908 Richter 1933 Edgeworth 1935	Ping 1932	Zavattari 1909 Ping 1932 Edgeworth 1935 Gnanamuthu 1937	
Phyllodactylus	Cope 1892			
Platydactylus			Sanders 1870 Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Ptychozoon	Richter 1933			
Stenodactylus			Gnanamuthu 1937	
Tarentola	Richter 1933		Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Thecodactylus			Kesteven 1944	Kesteven 1944
Uroplatus	Verslvys 1898, 1904 Camp 1923 Edgeworth 1935			
Dibamidae				
Dibamus	Rieppel 1981		Gasc 1968	
Iguanidae				
Ambryrhynchus	Avery & Tanner 1971	Avery & Tanner 1971	Avery & Tanner 1971	
Anolis	Cope 1892		Kesteven 1944	Willard 1918 Kesteven 1944
Basiliscus	Zavattari 1908	Gnanamuthu 1937	Gnanamuthu 1937	
Brachylophus	Camp 1923 Avery & Tanner 1971	Avery & Tanner 1971	Camp 1923 Avery & Tanner 1971	
Callisaurus	Cox & Tanner 1977		Cox & Tanner 1977	
Chalarodon	Avery & Tanner 1971	Avery & Tanner 1971	Avery & Tanner 1971	Renous-Lecuru 1972

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Chamaeleolis	Beddard 1907			
Conolophus	Avery & Tanner 1971	Avery & Tanner 1971	Avery & Tanner 1971	
Cophosaurus	Cox & Tanner 1977		Cox & Tanner 1977	
Crotaphytus	Cope 1892 Robison & Tanner 1962		Davis 1934 Robison & Tanner 1962	
Ctenosaura	Oelrich 1951 Avery & Tanner 1971	Oelrich 1956 Avery & Tanner 1971	Oelrich 1956 Avery & Tanner 1971	
Cyclura	Avery & Tanner 1971	Gandolfi 1908 Avery & Tanner 1971	Avery & Tanner 1971	
Dipsosaurus	Cope 1892 Avery & Tanner 1971	Avery & Tanner 1971	Avery & Tanner 1971	
Enyaliosaurus	Avery & Tanner 1971	Avery & Tanner 1971	Avery & Tanner 1971	
Holbrookia	Cox & Tanner 1977		Cox & Tanner 1977	
Iguana	Edgeworth 1935 Avery & Tanner 1971 Oldham & Smith 1975	Gandolfi 1908 Avery & Tanner 1971 Oldham & Smith 1975	Mivart 1867 Edgeworth 1935 Poglayen-Neuwall 1954 Avery & Tanner 1971 Oldham & Smith 1975	Poglayen-Neuwall 1954 Oldham & Smith 1975
Liolaemus		Gandolfi 1908		
Oplurus	Avery & Tanner 1971	Avery & Tanner 1971	Avery & Tanner 1971	
Phrynosoma	Cope 1892 Camp 1923 Richter 1933 Jenkins & Tanner 1968		Sanders 1874 Camp 1923 Jenkins & Tanner 1968	
Polychrus	Richter 1933			
Sauromalus	Avery & Tanner 1964, 1971	Avery & Tanner 1971	Avery & Tanner 1964, 1971	
Sceloporus	Cope 1892		Secoy 1971	
Tropidurus	Zavattari 1908 Edgeworth 1935		Zavattari 1908 Edgeworth 1935	
Uma	Cox & Tanner 1977		Cox & Tanner 1977	
Urosaurus	Fanghella, Avery & Tanner 1975		Fanghella, Avery & Tanner 1975	
Uta	Fanghella, Avery & Tanner 1975		Fanghella, Avery & Tanner 1975	

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Agamidae				
Agama	Edgeworth 1935 El-Toubi 1947 Harris 1963 Eyal-Giladi 1964	Gandolfi 1908	DeVis 1883 Lubosch 1933 Edgeworth 1935 Poglayen-Neuwall 1954 Harris 1963	Lubosch 1933 Poglayen-Neuwall 1954 Carpenter et al. 1977
Amphibolurus	Richter 1933	Gandolfi 1908	Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Calotes	Zavattari 1908 Camp 1923 Richter 1933 Edgeworth 1935 Iyer 1943	Gandolfi 1908 Sewerteoff 1929 Gnanamuthu 1937	Camp 1923 Gnanamuthu 1937 Poglayen-Neuwall 1954	Gnanamuthu 1937 Poglayen-Neuwall 1954
Ceratophora	Richter 1933			
Chlamydosaurus	Beddard 1905		DeVis 1883	Renous & Lecuru 1972
Cophotis	Richter 1933			
Draco	Richter 1933	Gnanamuthu 1937	Gnanamuthu 1937	
Hydrosaurus	Richter 1933			
Leiolepis	Richter 1933		Sanders 1872 Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Lyriocephalus	Richter 1933			
Otocryptis	Richter 1933			
Phrynocephalus	Richter 1933 Kesteven 1944	Sewertzoff 1929	Kesteven 1944	
Physignathus	Kesteven 1944		Kesteven 1944	Kesteven 1944
Sitana			Gnanamuthu 1937	
Uromastix	Islam 1955 Tilak 1964a,b		Furbringer 1922 Lubosch 1933 Edgeworth 1935 George 1948 Poglayen-Neuwall 1954 Throckmorton 1978	Poglayen-Neuwall 1954
Chamaeleonidae				
Chamaeleo	Zavattari 1908 Edgeworth 1935 Gnanamuthu 1937 Jollie 1960	Lubosch 1932 Gnanamuthu 1937	Mivart 1870 Mivart 1876 Zavattari 1908 Camp 1923 Lubosch 1933 Edgeworth 1935 Gnanamuthu 1937 Kesteven 1944 Poglayen-Neuwall 1954	Gnanamuthu 1937 Kesteven 1944 Poglayen-Neuwall 1954
Scincidae				
Ablepharus		Sewertzoff 1929		

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Chalcides	Richter 1933 El Toubi 1938 El Toubi & Kamal 1959a,b			Soliman & Hegazy 1971
Eumeces	Cope 1892 Zavattari 1908 Richter 1933 Nash & Tanner 1970		Zavattari 1908 Edgeworth 1935 Nash & Tanner 1970	
Lygosoma	Richter 1933			
Mabuya	Richter 1933 Gnanamuthu 1937 Tao & Ramaswami 1952	Gnanamuthu 1937	Gnanamuthu 1937	
Nessia	Richter 1933			
Riopa	Richter 1933			
Scincus	Richter 1933			
Tiligua	Beddard 1907		Lightoller 1939 Kesteven 1944 Poglayen-Neuwall 1954	Lightoller 1939 Poglayen-Neuwall 1954
Trachysaurus	Beddard 1907		Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Typhlosaurus	Rieppel 1981			
Cordylidae				
Cordylus	Beddard 1907 Camp 1923 Richter 1933 Edgeworth 1935		Camp 1923 Edgeworth 1935	
Gerrhosaurus	Camp 1923		Camp 1923	
Zonrus	Camp 1923			
Lacertidae				
Acanthodactylus	Richter 1933			
Cabrita		Gnanamuthu 1937	Gnanamuthu 1937	
Lacerta	Walter 1887 Zavattari 1908 Richter 1933 Edgeworth 1935	Sewertzoff 1929	Walter 1887 Camp 1923 Edgeworth 1935 Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Ophisops	Richter 1933			
Teiidae				
Ameiva	Richter 1933 Fisher & Tanner 1970	Minot 1880 Sewertzoff 1929 Presch 1971	Poglayen-Neuwall 1954 Fisher & Tanner 1970	Poglayen-Neuwall 1954

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Cnemidophorus	Cope 1892 Fisher & Tanner 1970	Presch 1971	Poglayen-Neuwall 1954 Fisher & Tanner 1970	Poglayen-Neuwall 1954
Neusticurus	Richter 1933			
Tupinambis	Zavattari 1908 Reese 1932 Edgeworth 1935 Jollie 1960		Zavattari 1908 Camp 1923 Edgeworth 1935 Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Anguinidae				
Anguis	Richter 1933	Sewertzoff 1929		
Gerrhonotus	Walter 1887 Cope 1892		Camp 1923 Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Ophiosaurus	Walter 1887	Sewertzoff 1929	Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Xenosauridae				
Shinosaurus	McDowell & Bogart 1954	McDowell & Bogart 1954	Haas 1960	
Xenosaurus	Camp 1923 McDowell & Bogart 1954	McDowell & Bogart 1954	Camp 1923 Haas 1960	
Helodermatidae				
Heloderma	Cope 1892 McDowell & Bogart 1954	McDowell & Bogart 1954	Camp 1923 Poglayen-Neuwall 1954	Poglayen-Neuwall 1954
Varanidae				
Varanus	Richter 1933 McDowell & Bogart 1954 Sondhi 1958	Sewertzoff 1929 McDowell & Bogart 1954 Sondhi 1958	Bradley 1903 Camp 1923 Edgeworth 1935 Gnanamuthu 1937 Lightoller 1939 Kesteven 1944 Poglayen-Neuwall 1954 Sondhi 1958	Watkinson 1906 Lightoller 1939 Kesteven 1944 Poglayen-Neuwall 1954
Lanthanotidae				
Lanthanotus	McDowell & Bogart 1954 McDowell 1972 Rieppel 1981	McDowell & Bogart 1954		
Anniellidae				
Anniella	Cope 1892 Rieppel 1981		Camp 1923	

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Amphisbaenidae				
Amphisbaena	Camp 1923 Richter 1933 Jollie 1960		Smalian 1885 Camp 1923	
Anopsibaena			Smalian 1885	
Bipes			Renous 1977 Smalian 1885	
Blanus			Smalian 1885	
Monopeltis	Richter 1933			
Rhineura	Cope 1892		Camp 1923	
Trogonophis			Smalian 1885	
Xantusidae				
Xantusia	Savage 1963 Cope 1892		Camp 1923	
Suborder Serpentes Anomalepididae				
Anomalepis	Smith & Warner 1948		Haas 1968	
Helminthophis	List 1966 Langebartel 1968		Langebartel 1968	Langebartel 1968
Liotyphlops	List 1966 Langebartel 1968		Langebartel 1968	Langebartel 1968
Typhlopidae				
Typhlops	List 1966 Langebartel 1968		Langebartel 1968	Langebartel 1968
Typhlophis	Evans 1955 List 1966	Evans 1955	Evans 1955	
Leptotyphlopidae				
Leptotyphlops	Smith & Warner 1948 List 1966 Langebartel 1968 Oldham, Smith & Miller 1970		Langebartel 1968 Oldham, Smith & Miller 1970	Langebartel 1968
Uropeltidae				
Platyplectrurus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Plectrurus	Rieppel 1981			
Rhinophis	Smith & Warner 1948 Langebartel 1968		Langebartel 1968	Langebartel 1968
Silybura	Langebartel 1968			
Uropeltis			Langebartel 1968	Langebartel 1968

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Aniliidae				
Anilius	Smith & Warner 1948 Langebartel 1968 Rieppel 1981		Langebartel 1968	Langebartel 1968
Cylindrophis	Smith & Warner 1948 Langebartel 1968		Lubosch 1933 Langebartel 1968	Lubosch 1933 Langebartel 1968
Xenopeltidae				
Xenopeltis	Smith & Warner 1948 Langebartel 1968		Langebartel 1968	Langebartel 1968
Boidae				
Aspidites	Smith & Warner 1948 Langebartel 1968			
Boa	Langebartel 1968		Gibson 1966	
Calabaria	Langebartel 1968		Langebartel 1968	Langebartel 1968
Charina	Langebartel 1968		Langebartel 1968	Langebartel 1968
Chondropython	Langebartel 1968			
Constrictor	Langebartel 1968		Langebartel 1968	Langebartel 1968
Enygrus	Langebartel 1968			
Epicrates	Langebartel 1968		Langebartel 1968	Langebartel 1968
Eryx	Smith & Warner 1948 Langebartel 1968		Langebartel 1968	Langebartel 1968
Eunectes	Langebartel 1968		Anthony & Serra 1950 Langebartel 1968	Langebartel 1968
Liasis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Lichanura	Langebartel 1968	Hershkowitz 1941		
Loxocemus	Smith & Warner 1948 Langebartel 1968			
Nardoana	Langebartel 1968			
Python	Furbringer 1922 Langebartel 1968 Oldham, Smith & Miller 1970		Lubosch 1933 Edgeworth 1935 Kesteven 1944 Frazzetta 1966 Langebartel 1968 Oldham, Smith & Miller 1970	Lubosch 1933 Kesteven 1944 Langebartel 1968
Sanzinia	Langebartel 1968		Langebartel 1968	Langebartel 1968
Trachyboa	Langebartel 1968		Langebartel 1968	Langebartel 1968

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Colubridae				
Achalinus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Achrochordus	Smith & Warner 1948 Langebartel 1968		Langebartel 1968	Langebartel 1968
Adelphicus	Langebartel 1968			
Amblycephalus	Smith & Warner 1948 Langebartel 1968		Langebartel 1968	Langebartel 1968
Aparallactus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Apostolepis	Langebartel 1968			
Atretium	Langebartel 1968		Langebartel 1968	Langebartel 1968
Boiga	Langebartel 1968			
Carphophis	Smith & Warner 1948 Langebartel 1968			
Cerberus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Chersodromus	Langebartel 1968			
Chersydrus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Chrysopelea	Langebartel 1968			
Clelia	Langebartel 1968			
Coluber	Walter 1887 Langebartel 1968		Walter 1887	
Coniophanes	Langebartel 1968			
Conophis	Langebartel 1968			
Conepsis	Langebartel 1968			
Crotaphopeltis	Langebartel 1968			
Cyclagras	Langebartel 1968			
Dasypeltis	Smith & Warner 1948 Langebartel 1968		Langebartel 1968	Langebartel 1968
Dendrophidion	Langebartel 1968			
Diadophis	Langebartel 1968			
Dipsadotoa	Langebartel 1968			
Dispholidus	Langebartel 1968			
Dromophis	Langebartel 1968			
Drymarchon	Langebartel 1968			
Drymobius	Langebartel 1968			
Dryophis	Langebartel 1968		Lubosch 1933	
Elaphe	Langebartel 1968	Morgans & Heidt 1978	Albright & Nelson 1959 Langebartel 1968	Langebartel 1968 Auen & Langebartel 1977
Elapomorphus	Langebartel 1968			
Elapops	Langebartel 1968			

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Enhydrus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Enulius	Langebartel 1968			
Farancia	Langebartel 1968			
Ficimia	Langebartel 1968			
Fimbrios	Langebartel 1968		Langebartel 1968	Langebartel 1968
Geophis	Langebartel 1968			
Haldea	Langebartel 1968			
Haplopeltura	Langebartel 1968		Langebartel 1968	Langebartel 1968
Heterodon	Weaver 1965 Langebartel 1968		Langebartel 1968	Langebartel 1968
Homalopsis	Langebartel 1968			
Lampropeltis	Langebartel 1968			
Leptodeira	Langebartel 1968			
Leptophis	Langebartel 1968			
Manolepis	Langebartel 1968			
Masticophis	Langebartel 1968			
Mehelya	Langebartel 1968		Langebartel 1968	Langebartel 1968
Natrix	Sondhi 1958	Sondhi 1958	Sondhi 1958	Sondhi 1958
Nerodia	Langebartel 1968 Oldham, Smith & Miller 1970	Morgans & Heidt 1978 Varkey 1979	Langebartel 1968 Oldham, Smith & Miller 1970 Varkey 1979	Langebartel 1968 Varkey 1979
Ninia	Langebartel 1968			
Nothopsis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Opheodrys	Langebartel 1968 Cundall 1974		Cundall 1974	
Oxybelis	Langebartel 1968			
Oxyrhabdinium	Langebartel 1968			
Pituophis	Smith & Warner 1948 Bullock & Tanner 1966 Langebartel 1968 Oldham, Smith & Miller 1970		Oldham, Smith & Miller 1970	
Psamnodynastes	Langebartel 1968			
Rhadineae	Langebartel 1968			
Rhadinelia	Langebartel 1968			
Rhinocheilus	Langebartel 1968			
Salvadora	Langebartel 1968			
Sibynomorphus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Sonora	Langebartel 1968			
Tantilla	Langebartel 1968			

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Thamnophis	Bullock & Tanner 1966 Langebartel 1968 Oldham, Smith & Miller 1970		Langebartel 1968 Oldham, Smith & Miller 1970	Langebartel 1968 Aven & Langebartel 1977
Toluca	Langebartel 1968			
Trimorphodon	Langebartel 1968			
Tropidonotus	Langebartel 1968	Sewertzoff 1929	Lubosch 1933	Lubosch 1933
Xenodermus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Xenodon	Weaver 1965		Anthony & Serra 1949 Langebartel 1968	Langebartel 1968
Elapidae				
Acanthophis	Langebartel 1968			
Aspidelaps	Langebartel 1968			
Bungarus	Langebartel 1968			
Calliophis	Langebartel 1968			
Demansia	Langebartel 1968			
Dendrospis	Langebartel 1968			
Denisonia	Langebartel 1968		Langebartel 1968	Langebartel 1968
Doliophis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Elaps	Langebartel 1968			
Elapsoidea	Langebartel 1968			
Furina	Langebartel 1968			
Hemachatus	Langebartel 1968			
Hemibungarus	Langebartel 1968			
Leptomicrurus	Langebartel 1968			
Maticora	Langebartel 1968			
Micruroides	Langebartel 1968			
Micrurus	Smith & Warner 1948 Langebartel 1968			
Naja	Langebartel 1968 Kamal, Hamouda & Mokhtar 1970		Lubosch 1933 Langebartel 1968	Langebartel 1968
Notechis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Ogmodon	Langebartel 1968			
Pseudechis			Kesteven 1944	Kesteven 1944
Pseudelaps	Langebartel 1968			
Ultocalamus	Langebartel 1968			

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Hydrophidae				
Aipysurus	Langebartel 1968		Langebartel 1968	Langebartel 1968
Hydrophis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Kerilia	Langebartel 1968			
Lapemis	Smith & Warner 1948 Langebartel 1968			
Laticauda	Langebartel 1968		Langebartel 1968	Langebartel 1968
Pelamis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Thalasophina	Langebartel 1968			
Viperidae				
Aspis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Atheris	Langebartel 1968			
Atractaspis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Bitis	Langebartel 1968			
Causus	Langebartel 1968		Haas 1952 Langebartel 1968	Langebartel 1968
Cerastes	Langebartel 1968		Langebartel 1968	Langebartel 1968
Echis	Langebartel 1968		Langebartel 1968	Langebartel 1968
Pseudocerastes	Langebartel 1968			
Vipera	Furbringer 1922 Langebartel 1968		Edgeworth 1935 Langebartel 1968	Langebartel 1968
Crotalidae				
Agkistrodon	Smith & Warner 1948 Langebartel 1968		Langebartel 1968 Kardong 1973	Langebartel 1968
Bothrops	Langebartel 1968		Langebartel 1968	Langebartel 1968
Crotalus	Langebartel 1968 Oldham, Smith & Miller 1970		Langebartel 1968 Oldham, Smith & Miller 1970	Langebartel 1968
Lachesis	Langebartel 1968		Lubosch 1933 Langebartel 1968	Lubosch 1933 Langebartel 1968
Sistrurus	Langebartel 1968			
Trimeresurus	Langebartel 1968			
Order Crocodilia **Crocodylidae**				
Alligator	Reese 1915 Furbringer 1922 Edgeworth 1935 Chiason 1962	Sewertzoff 1929	Reese 1915 Lubosch 1933 Edgeworth 1935 Chiason 1962 Poglayen-Neuwall 1953b	Reese 1915 Lubosch 1933 Poglayen-Neuwall 1953b
Caiman	Schumacher 1973		Schumacher 1973	Schumacher 1973

Table 1 continued.

Genus	Hyoid	Tongue	Musculature	Nerves
Crocodylus	Furbringer 1922 Sondhi 1958 Frank & Smit 1974	Sewertzoff 1929 Sondhi 1958	Camp 1923 Edgeworth 1935 Kesteven 1944 Sondhi 1958 Poglayen-Neuwall 1953b	Kesteven 1944 Poglayen-Neuwall 1953b
Gavialidae				
Gavialis	Furbringer 1922 Sondhi 1958	Sondhi 1958	Sondhi 1958	Sondhi 1958

attempts have not led to a completely satisfactory understanding of the hyoid derivatives, and the homologies of the hyoid constituents cannot be ascertained without comparative embryological information on the development of the reptiles' buccal floor. Thus, our interpretation of the hyoids of reptiles should be considered tentative at best.

The tentativeness of our present understanding of the homologies of many of these structures, when considered for the reptiles as a whole, is indicated in a recent study by Frank and Smit (1974). They consider the early ontogeny of the columella auris of *Crocodylus niloticus*, and its relationship to the reptilian hyoid arch is reviewed and discussed in detail. Considerable effort is expended in the clarification of terms and in the description of particular morphological structures that have been in some confusion as a result of misunderstandings. Frank and Smit (1974) were trying to establish a model to be used, and to stimulate subsequent research. We hope that such studies will be undertaken and will clarify structural homologies for each of the remaining arches occurring in reptiles. Ontogenetic studies leading to an understanding not only of reptiles in general but also of each reptilian order are needed before we can consistently assign exact anatomical limits to structures and provide an appropriate name for each morphological entity. Until such are available, however, we must remain within the limits of our present knowledge.

The hyoid apparatus of reptiles has been described by Romer (1956) as having a median ventral piece, the copula, which forms the body of the hyoid (= corpus hyoidem BH). Extending anteriorly from the corpus hyoideum is a medial process, the processus lingualis (= processus entoglossus PL), which terminates in the substance of the tongue. Laterally the corpus gives off three paired horns or cornua that extend posterodorsally around the throat, ending freely or attached to the stapedial structures. The anteriormost pair of cornua are the hyoid cornua (HC), which, at their distal ends, articulate with the most lateral of the hyoid bars or epihyals (EH). The second pair of cornua are elongated bars (usually cartilagenous) forming the first ceratobranchials (CBI) and attaching distally to the epihyals by way of short cartilaginous bars on each side of the first epibranchials (EBI). The third and last processes of the corpus hyoideum are a pair of posteriorly extending rods, the second epibranchials (EBII), a pair of short cartilaginous bars that articulate by their distal ends with the epibranchials of the first and second arches (Figs. 1–3).

The association of the hyoid with, and its attachment to, the skull is of evolutionary importance. In primitive lizards, such as some Gekkonidae, the hyoid is attached to the extracolumella. Thus the hyoid apparatus maintains its association with the stapedial structures that may be derived from its dorsal extremities. This point of union is or is not persistent as indicated by Versluys (1898 and 1904) and, in some individuals, is transferred to the paraoccipital process of the opisthotic bone.

The possession of all three cornua is considered the primitive condition and is demonstrated in *Sphenodon*, where all the cornua are long, slender, and well-developed structures. A few gekkos and xantusiids have an incomplete third arch with a slight break between ceratobranchial II and epibranchial II. In the Iguanidae (Avery and Tanner 1971) all three arches are present, but lack their distal connections in some cases.

Rhynchocephalia

The hyoid of *Sphenodon* has been discussed by Osawa (1898, Howes and Swinnerton 1901, Furbringer 1922, Edgeworth 1931, 1935, and Rieppel 1978.

The hyoid apparatus of *Sphenodon* (Fig. 1) is simple with all elements present. The basihyoid is broad with a short lingual process extending anteriorly. Laterally the basihyoid extends as projections corresponding to the hyoid cornua but not distinctly separate from the basihyoid. At their distal ends, the cornua articulate with epihyals that extend straight posteriorly. The basihyoid also has a pair of posterior projections, the second ceratobranchials, that are widely separated and curve laterally at their distal ends. The first ceratobranchials articulate with the basihyoid lateral to the point of origin of the second ceratobranchials. They curve and closely approach the distal ends of the epihyals. Rieppel (1978) illustrated the hyoid apparatus and its associated muscles. A taxonomic survey provides a general overview of this order:

Chelonia

The hyoid apparatus of turtles has been described by the following:

Chelidae
Chelodina (Furbringer 1922)

Dermatemydidae
Dermatemys (Furbringer (1922)

Chelydridae
Cheydra (Furbringer 1922, Edgeworth 1935, Schumacher 1973), *Kinosternon* (Furbringer 1922, Schumacher 1973), *Sternotherus* (Furbringer 1922, Schumacher 1973), *Chrysemys* (Furbringer 1922, Ashley 1955, Schumacher 1973), *Cuora* (Furbringer 1922), *Clemmys* (Siebenrock 1898, Furbringer 1922, Schumacher 1973), *Emys* (Walter 1887, Furbringer 1922, Schumacher 1973), *Geochelone* (Bojanus 1819, Furbringer 1922, Edgeworth 1935, Schumacher 1973), *Terrapene* (Furbringer 1922).

Trionychidae
Lissemys (Furbringer 1922, Sondhi 1958, Schumacher 1973), *Trionyx* (Siebenrock 1898, Sondhi 1958, Furbringer 1922, Schumacher 1973).

Cheloniidae
Caretta (Furbringer 1922, Schumacher 1973).

Dermochelyidae
Dermochelys (Schumacher 1973).

Schumacher (1973) has treated the hyoids of turtles and crocodilians extensively in this series, so our discussion will serve as a general review.

The hyoid apparatus of turtles has been described briefly by Bojanus (1819) and figured by Mitchell and Morehouse (1863). More

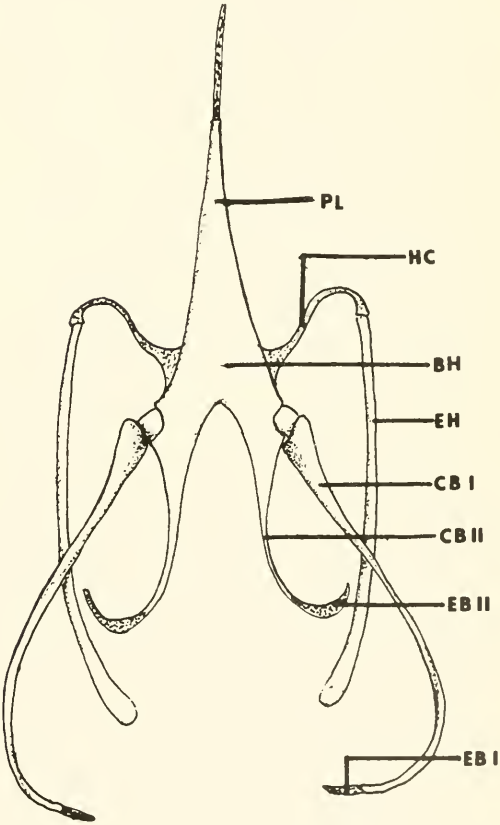


Fig. 1. Hyoid apparatus of *Sphenodon punctatum* (USUN 029429): BH-body of hyoid, (basihyoid) CB1-first ceratobranchial, CB11-second ceratobranchial, EB1-first epibranchial, EB11-second epibranchial, EH-epihyal, HC-hyoid cornu, PL-processus lingualis.

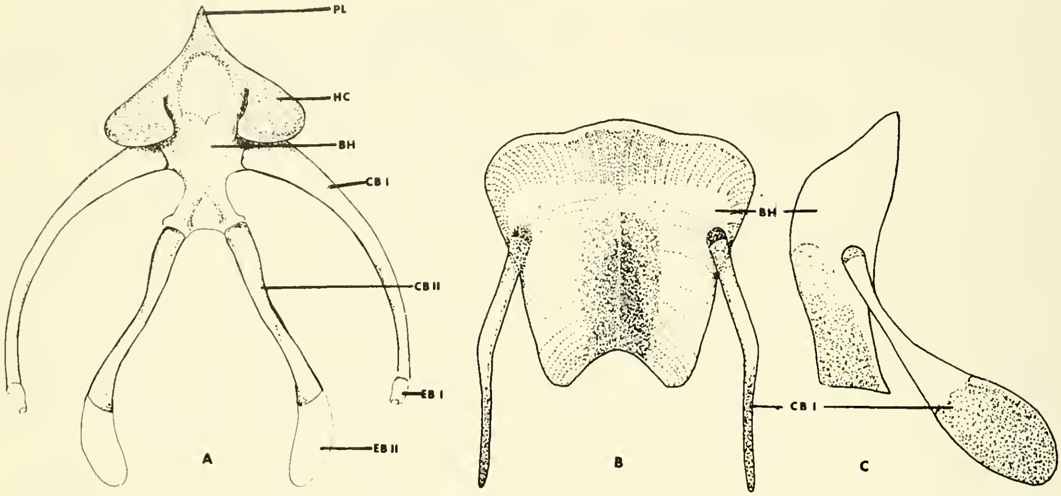


Fig. 2.—Hyoid apparatus of A, *Chelydra serpentina* (Southern Connecticut State College, 598), ventral view; B, *Caiman sclerops*, ventral view; C, *Caiman sclerops*, lateral view (SCSC 585).

complete reports include those of Siebenrock (1898), Furbringer (1922), Versluys (1936), Gnanamuthu (1937), and Sondhi (1958). The hyoid is more ossified than that of most lizards and snakes.

In *Trionyx* and *Lissemys* the hyoid has a body with a lingual process equipped with a hypoglossum (Sondhi 1958); this is a leaflike plate of cartilage loosely attached to its ventral side. The hyoid cornua are greatly reduced and form knoblike projections from the body. The second ceratobranchials extend posteriorly from the body as subcylindrical structures.

The body of the hyoid is composed of three pairs of serially arranged cartilaginous blocks. The most anterior part has on its lateral margins very short anterior projections. The middle pair of plates bear the articulating surfaces for the hyoid cornua. The posterior pair of plates are completely fused to the middle pair and have between them and the middle plates a diamond-shaped interspace. Posteriorly the last pair of plates provides facets for the articulations of the second ceratobranchials. In *Chelydra* the hyoid is more solidly constructed, consisting of bone except for its anterior end, the ceratohyals, and the epihyals, which are cartilage (Fig. 2 A).

The possession of a hypoglossum by turtles appears to be unique. The structure was first described by Stannius (1856) as an entoglossum. The term *hypoglossum* was first used by Furbringer (1922), who described it as the part not entering the tongue. Nick (1913) and Versluys (1936) observed that in turtles, with the exception of *Dermochelys*, the hypoglossum is platelike, unpaired, and lies ventral to the lingual process. Nick (1913) also suggests that the hypoglossum is a chondrification of connective tissue of the tendinous plate. The hypoglossum is extensive in *Trionyx*, in which it may have two slender posterior strips or be an elongate plate, rounded at each end and extending anteriorly from the middle components of the body of the hyoid almost to the symphysis of the mandible. Sondhi (1958) suggested that the hypoglossum functions to raise or lower the buccal floor by means of two muscles (Mm. entoglosso-hypoglossalis and hypoglosso-lateralis) attached to its dorsal surface and extending to the processus entoglossus and the buccal floor. In other genera, *Chelydra*, *Chrysemys*, *Pseudemys*, and *Sternotherus*, it is proportionally smaller and varies in shape (Fig. 3). Hacker and Schumacher (1955) figure it for *Testudo* and describe the M. entoglosso-glossus that serves as an attachment between the hypoglossum and the processus lingualis. In *Gopherus agassizi*, the hypoglossum is elongate and slender with a median ridge ventrally and a convexity dorsally. It is closely associated with the processus lingualis. A paired muscle (M. entoglossoglossus) is attached to its dorsal surface on

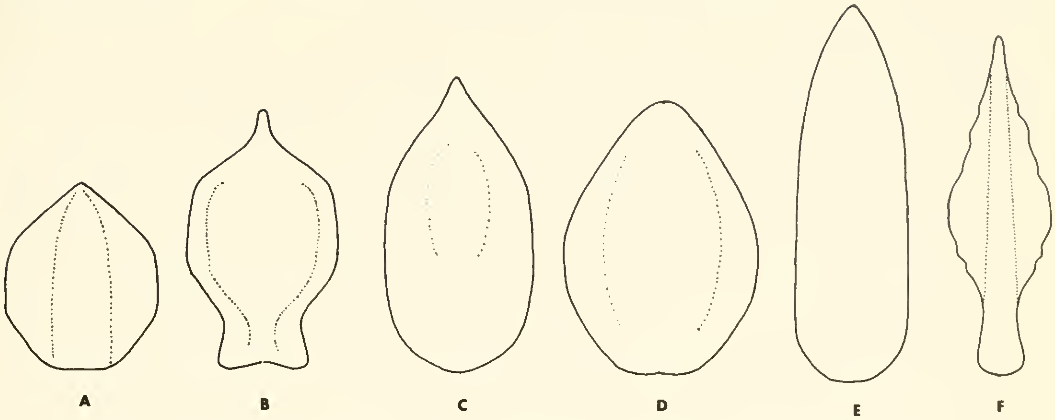


Fig. 3. The hypoglossum of five genera of turtles, ventral views: A, *Chrysemys picta* (SCSC 602); B, *Sternotherus odoratus* (SCSC 476); C, *Pseudemys scripta* (BYU 40343); D, *Chelydra serpentina* (BYU 33642); E, *Trionyx spinifera* (SCSC 596); F, *Gopherus agassizi* (BYU 30084).

each side, just lateral to the median concavity. These muscles extend dorsally and anteriorly to insert in the connective tissues surrounding the processus lingualis. The pointed anterior end of the hypoglossum extends beyond the end of the processus lingualis.

In the few examples we have seen, the hypoglossum of terrestrial tortoises appears to be more slender and with better developed muscular attachments to the hyoid apparatus than in other turtles.

The hyoid cornua are short cartilaginous knobs covered ventrally by the M. ceratohyoideum. The first ceratobranchials are long, subcylindrical, rodlike bones that articulate with the middle component of the body of the hyoid. They extend posteriorly to curve dorsally and partially surround the neck, where they lie embedded in the M. ceratohyoideus.

The second ceratobranchials are composed of proximal bony parts and distal cartilaginous parts. The distal ends girdle the posterior part of the neck and lie beneath the M. omohyoideum. A ligament connects the base of each second ceratobranchial with the anterior part of each hyoid cornu.

Crocodilia

In *Alligator, Crocodylus,* and *Gavialis* the hyoid apparatus consists of the body of the hyoid and a pair of posterior projections. The hyoid cornua and all other processes are absent. Sondhi (1958) has described the structures in *Gavialis* in detail. The body of the hyoid is the most prominent part of the apparatus and forms an inverted triangular cartilaginous plate. There is a deep notch in the posterior margin, and laterally it bears a facet for the articulation of the posterior projection. The hyoid lies dorsal to the M. mylohyoideus, ventral to the glottis, and anterior to part of the trachea. Anteriorly the body is covered in part by the Mm. hyoglossus and genioglossus. The posterior projections are rodlike, cartilaginous, and extend posteromedially, gradually becoming flattened, compressed, and twisted. A ligament connects these projections with fused rodlike structures closely adhering to the posterolateral borders of the body and probably corresponding to the second ceratobranchials of other reptiles.

The above description of *Gavialis* corresponds to our findings in *Caiman* except that the body of the hyoid of the latter is not triangular, but broadly rectangular and, from a dorsal view, similar to a wide-bladed shovel (Fig. 2-B,C). There is a shallow notch posteriorly, and the posterior projections are bone proximally and expand into flat sheets of cartilage distally. We did not find a ligament extending dorsolaterally onto the cervical area from the ends of the posterior projections.

Lacertilia

The hyoid of lizards has been examined by the following:

Gekkonidae

Cnemaspis (Richter 1933), *Coleonyx* (Camp 1923, Kluge 1962), *Eublepharis*

TABLE 2. Publications, not previously cited, dealing with topics peripheral to the buccal floor.

A. Osteology

- 1. Chelonia
  - Ashley 1955, *Chelydra, Chrysemys*
  - Goppert 1903, *Testudo*

- 2. Rhynchocephalia
  - Goppert 1900, *Sphenodon*
  - Lakjer 1927, *Sphenodon*
  - Rieppel 1979, 1981, *Sphenodon*

- 3. Lacertila
  - Barrows and Smith 1947, *Xenosaurus*
  - Beddard 1905a, *Uromastix*
  - Bellairs 1950, *Anniella*
  - Criley 1968, *Barisia, Elgaria, Gerrhonotus*
  - Duda 1965, *Agama*
  - El Toubi 1938, *Scincus*
  - El Toubi 1947a, *Agama*
  - El Toubi 1947b, *Uromastix*
  - El Toubi and Kamal 1959a, *Chalcides*
  - El Toubi and Kamal 1959b, *Chalcides*
  - Elyal-Giladi 1964, *Agama, Chalcides*
  - George 1954, *Uromastix*
  - Goppert 1903, *Amphisbaena, Calotes, Cnemidophorus, Lacerta, Mabuya, Platydactylus*
  - Iyer 1942, *Calotes*
  - Iyer 1943, *Calotes*
  - Kingman 1932, *Eumeces*
  - Lakjer 1927, *Ameiva, Anguis, Amphisbaena, Calotes, Chalcides, Chamaelo, Cordylus, Eumeces, Gekko, Hyperodapedon, Heloderma, Iguana, Lialis, Lygosoma, Phrynosoma, Pygopus, Lacerta, Tiligua, Trogonophis, Uromastix, Varanus*
  - Mahendra 1949, *Hemidactylus*
  - Malam 1941, *Gerrhosaurus*
  - Norris and Lowe 1951, *Phrynosoma*
  - Parker 1880, *Lacerta, Agama*
  - Rathor 1969, *Ophiomorus*
  - Rice 1920, *Eumeces*
  - Siebenrock 1892a, *Uroplatus*
  - Siebenrock 1892b, *Scincus*
  - Siebenrock 1893, *Brooksesia*
  - Siebenrock 1894, *Lacerta*
  - Siebenrock 1895, *Agama*
  - Sinitsin 1928, *Alopogloscus, Ameiva, Anadia, Bachia, Callopistes, Cercosaura, Centropyx, Cnemidophorus, Dracaena, Dicrodon, Echinosaura, Ecleopus, Euspondylus, Gymnophthalmus, Iphisa, Leposoma, Neusticurus, Ophiognomon, Pantodactylus, Prionodactylus, Pholidobolus, Pructoporus, Scolecosaurus, Teius, Tretioscincus, Tupinambis*
  - Tilak 1964a, *Uromastix*
  - Toerien 1950, *Anniella*
  - Webb 1951, *Oedura, Palmatogecko*
  - Weiner and Smith 1965, *Crotaphytus*
  - Young 1942, *Xantusia*
  - Zangerl 1944, *Amphisbaena, Bipes, Geocalamus, Leptosternon, Monopelitis, Rhineura, Trogonophis*

Table 2 continued.

- 4. Ophidia
  - Berman 1961, *Echis, Vipera*
  - Berman 1965, *Calamaria*
  - Boltt and Ewer 1954, *Bitis*
  - Dullemeijer 1956, *Vipera*
  - Dullemeijer 1959, *Bitis, Crotalus, Trimeresurus, Vipera*
  - Kardong 1974, 1977, *Agkistrodon*
  - Liem, Mark and Rabb 1971, *Azemiops*
  - Goppert 1903, *Python, Tropidonotus*
  - McKay 1889, *Acanthrophis*
  - Rosenberg 1968, *Bungarus*
  - Varkey 1979, *Nerodia*

- 5. Crocodilia
  - Chiasson 1962, *Alligator*
  - Goppert 1903, *Crocodylus*

B. Myology

- 1. Chelonia
  - Adams 1919, *Chelydra*
  - Ashley 1955, *Chelydra, Chrysemys*
  - Schumacher 1956, *Amyda, Chelodina, Chelonia, Caretta, Clemmys, Dogania, Emydura, Emys, Eretmochelys, Graptemys, Hardella, Macrochelys, Hydromedusa, Pelomedusa, Pelusios, Platysternon, Podocnemis, Testudo, Trionyx*
  - Shah 1963, *Chelodina, Deirochelys*

- 2. Rhynchocephalia
  - Adams 1919, *Sphenodon*
  - Rieppel 1978, *Sphenodon*

- 3. Lacertila
  - Adams 1919, *Iguana, Varanus*
  - Bradley 1903, *Agama, Gekko, Lacerta, Pseudopus, Varanus*
  - Brock 1938, *Gymnodactylus*
  - Davis 1934, *Crotaphytus*
  - George 1948, *Uromastix*
  - Iordansky 1970, *Agama, Cordylus, Eumeces, Gekko, Lacerta, Ophiosaurus, Teratoscincus, Varanus*
  - Norris and Lowe 1951, *Phrynosoma*
  - Rathor 1969, *Ophiomorus*
  - Tornier 1904, *Chamaeleo*

- 4. Ophidia
  - Adams 1925, *Natrix*
  - Bergman 1961, *Echis, Vipera*
  - Bergman 1965, *Calamaria*
  - Boltt and Ewer 1954, *Bitis*
  - Cowan and Hick 1951, *Thamnophis*
  - Dullemeijer 1956, *Vipera*
  - Dullemeijer 1959, *Bitis, Crotalus, Trimeresurus, Vipera*
  - Haas 1930, *Amblycephalus, Calbaria, Calamaria, Cylindrophis, Eryx, Ilysia, Oxybelis, Silybura, Xenopeltis*
  - Haas 1931a, *Acrochordus, Amblycephalus, Atractaspis, Atractus, Bungarus, Calabaria, Cala-*

Table 2 continued.

maria, Causus, Cerberus, Chersydrus, Cylindrophis, Dasypeltis, Dispsadomonphus, Elaps, Eryx, Glauconia, Ilysia, Lachesis, Leptognathus, Naja, Oxybelis, Pelamis, Python, Polyodontophis, Silyura, Typhlops, Xenodon, Xenopeltis
Haas 1931b, *Acrodordus, Atractaspis, Causus, Cerberus, Chersydrus, Cylindrophis, Dasypeltis, Dispholidus, Leptognathus, Petalognathus, Polyodontophis, Scaphiophis, Xenodon*
Haas 1952, *Causus*
Heymans 1970, *Natrix*
Heymans 1975, *Aparallactus, Atractaspis, Chilorhinophis*
Kochva 1958a, *Vipera*
Kochva 1958b, *Agkistrodon, Aspis, Atheris, Atractaspis, Bitis, Bothrops, Causus, Crotalus, Echis, Natrix, Naja, Ophiophagus, Pseudocerastes, Vipera, Walterinnesia*
Kardong 1974, *Agkistrodon*
Liem, Mark, and Rabb 1971, *Azemiops*
McKey 1889, *Acanthrophis*
Rosenberg 1968, *Bungarus*
Rosenberg and Gans 1976, *Elachistodon*

5. *Crocodilia*
Adams 1919, *Alligator*
Chiasson 1962, *Alligator*

C. Miscellaneous

1. Chelonia
Johnson 1922, Branchial pouch derivatives, *Chelydra, Chrysemys*
Goppert 1900, Larynx, *Chelonia, Dermochelys, Emys, Testudo*
Siebenrock 1900, Larynx, *Testudo*

2. Lacertila
Goppert 1900, Larynx, *Amphisbaena, Platydactylus, Tiliqua*
Perrier 1902, Thymus and thyroid glands, *Lacerta*
Saint-Remy and Prenant 1904, Thymus and thyroid glands, *Anguis, Lacerta*
Sidkey 1967, Carotid Sinus, *Chalcides, Scincus*

3. Ophidia
Goppert 1900, Larynx, *Coronella, Python, Tropidonotus*
Kroll 1973, Taste buds, *Leptotyphlops*
Saint-Remy and Prenant 1904, Thymus and thyroid glands, *Coluber, Tropidonotus*
Van Bourgondien and Bother 1969, Cephalic arterial patterns, *Agkistrodon, Crotalus, Lachesis, Sistrurus*

4. Crocodilia
Goppert 1900, Larynx, *Crocodylus*
Siebenrock 1899, Larynx, *Crocodylus*

(Cope 1892, Camp 1923), *Gekko* (Camp 1923, Richter 1933), *Gehydra* (Richter 1933), *Gymnodactylus* (Richter 1933), *Hemidactylus* (Zavattari 1908, Richter 1933, Edgeworth 1935), *Phyllodactylus* (Cope 1892), *Ptychozoon* (Richter 1933), *Tarentola* (Richter 1933), *Uroplatus* (Versluys 1898, 1904, Camp 1923, Edgeworth 1935).

Dibamidae
Dibamus (Rieppel 1981).

Iguanidae
Amblyrhynchus (Avery & Tanner 1971), *Anolis* (Cope 1892), *Basiliscus* (Zavattari 1908), *Brachylophus* (Camp 1923, Avery & Tanner 1971), *Callisaurus* (Cox & Tanner 1977), *Chalarodon* (Avery & Tanner 1971), *Chamaeleolis* (Beddard 1907), *Conolophus* (Avery & Tanner 1971), *Cophosaurus* (Cox & Tanner 1977), *Crotaphytus* (Cope 1892, Robison & Tanner 1962), *Ctenosaura* (Oelrich 1956, Avery & Tanner 1971), *Cyclura* (Avery & Tanner 1971), *Dipsosaurus* (Cope 1892, Avery & Tanner 1971), *Enyaliosaurus* (Avery & Tanner 1971), *Holbrookia* (Cox & Tanner 1977), *Iguana* (Edgeworth 1935, Avery & Tanner 1971, Oldham & Smith 1945), *Oplurus* (Avery & Tanner 1971), *Phrynosoma* (Cope 1892, Camp 1923, Richter 1933, Jenkins & Tanner 1968), *Polychrus* (Richter 1933), *Sauromalus* (Avery & Tanner 1964, 1971), *Sceloporus* (Cope 1892), *Tropidurus* (Zavattari 1908, Edgeworth 1935), *Uma* (Cox & Tanner 1977), *Urosaurus* (Fanghella, Avery & Tanner 1975), *Uta* (Fanghella, Avery & Tanner 1975).

Agamidae
Agama (Edgeworth 1935, El Toubi 1947, Harris 1963, Eyal-Giladi 1964), *Amphibolurus* (Richter 1933), *Calotes* (Zavattari 1908, Camp 1923, Richter 1933, Edgeworth 1935, Iyer 1943), *Ceratophura* (Richter 1933), *Chlamydosaurus* (Beddard 1905), *Cophotis* (Richter 1933), *Draco* (Richter 1933), *Hydrosaurus* (Richter 1933), *Leiolepis* (Richter 1933), *Lyriocephalus* (Richter 1933), *Otocryptis* (Richter 1933), *Phrynocephalus* (Richter 1933, Kesteven 1944), *Physignathus* (Kes-

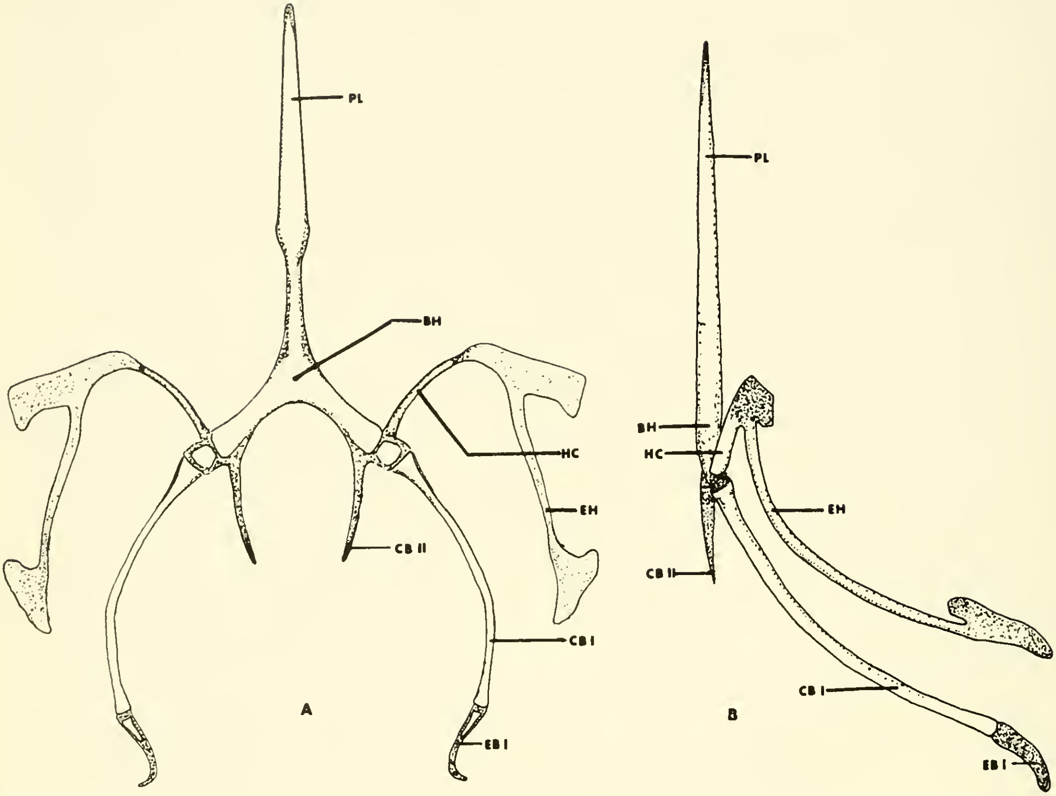


Fig. 4. Hyoid apparatus of *Tarentola annularis* (BYU 18123): A, ventral view; B, lateral view.

teven 1944), *Uromastix* (Islam 1955, Tilak 1964a,b).

Chamaeleonidae

Chamaeleo (Zavattari 1908, Edgeworth 1935, Gnanamuthu 1937, Jollie 1960).

Scincidae

Acontias (Rieppel 1981), *Acontophiops* (Rieppel 1981), *Chalcides* (Richter 1933, El Toubi 1938, El Toubi & Kamal 1959a,b), *Eumeces* (Cope 1892, Zavattari 1908, Richter 1933, Nash & Tanner 1970), *Lygosoma* (Richter 1933), *Mabuya* (Richter 1933, Gnanamuthu 1937, Rao & Ramaswami 1952), *Nessia* (Richter 1933), *Riopa* (Richter 1933), *Tiliqua* (Beddard 1907), *Scincus* (Richter 1933), *Trachysaurus* (Beddard 1907), *Typhlosaurus* (Rieppel 1981).

Cordylidae

Cordylus (Beddard 1907, Camp 1923, Richter 1933, Edgeworth 1935), *Gerrhosaurus* (Camp 1923), *Zonurus* (Camp 1923).

Lacertidae

Acanthodactylus (Richter 1933), *Lacerta* (Walter 1887, Zavattari 1908, Richter 1933, Edgeworth 1935), *Ophisops* (Richter 1933).

Teiidae

Ameiva (Richter 1933, Fisher & Tanner 1970), *Cnemidophorus* (Cope 1892, Fisher & Tanner 1970), *Neusticurus* (Richter 1933), *Tupinambis* (Zavattari 1908, Reese 1932, Edgeworth 1935, Jollie 1960).

Anguinidae

Anguis (Richter 1933), *Gerrhonotus* (Walter 1887, Cope 1892), *Ophiosaurus* (Walter 1887).

Xenosauridae

Shinosaurus (McDowell & Bogert 1954), *Xenosaurus* (McDowell & Bogert 1954, McDowell 1972).

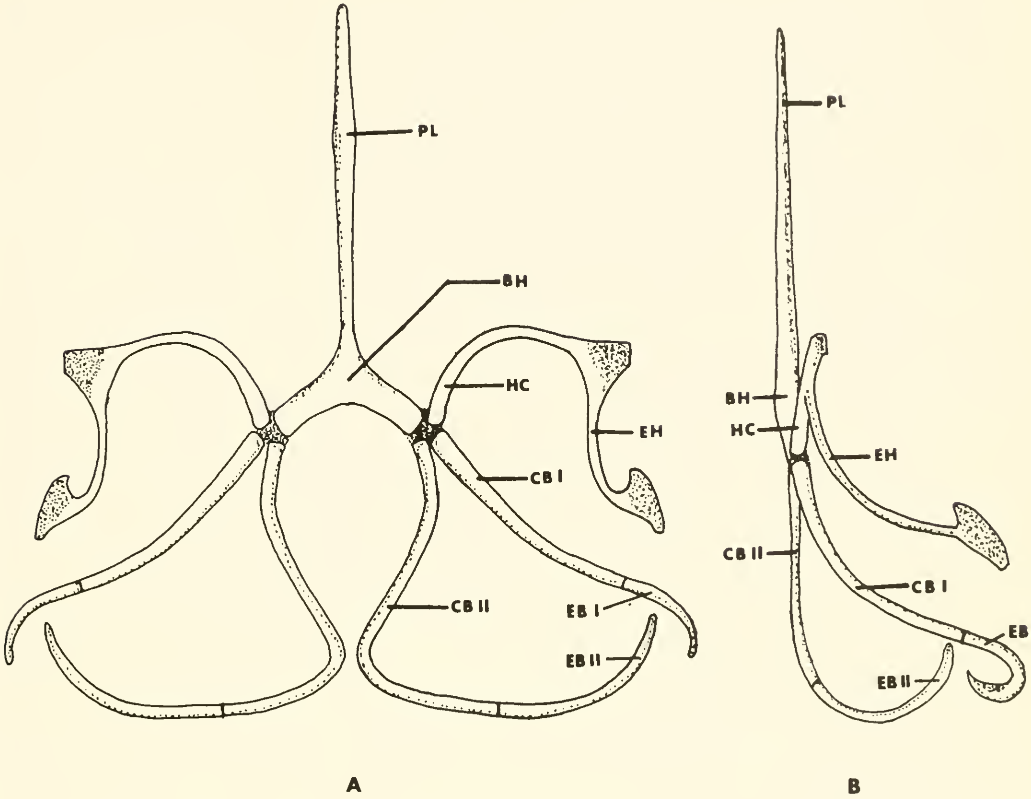


Fig. 5. Hyoid apparatus of *Coleonyx variegatus* (BYU 18796): A, ventral view; B, lateral view.

Helodermatidae
Heloderma (Cope 1892, McDowell & Bogert 1954).

Varanidae
Varanus (Richter 1933, McDowell & Bogert 1954, Sondhi 1958).

Lanthanotidae
Lanthanotus (McDowell & Bogert 1954, Rieppel 1981).

Anniellidae
Anniella (Cope 1892, Rieppel 1981).

Anphisbaenidae
Amphisbaena (Camp 1923, Richter 1933, Jollie 1960), *Monopeltis* (Richter 1933), *Rhineura* (Cope 1892).

Xantusidae
Xantusia (Cope 1892, Savage 1963).

Most lizards have a hyoid consisting of a basihyal (corpus hyoideum) with a pair, each, of anterior and posterior cornua as described by Cope (1892), Zavattari (1908), Furbringer (1922), Camp (1923), Versluys (1936), DeBeer (1937), Gnanamuthu (1937), Mahendra (1947), Rao and Ramaswami (1952), McDowell and Bogert (1954), Oelrich (1956), Romer (1956), Sondhi (1958), Jollie (1960), Robison and Tanner (1962), Avery and Tanner (1964), Jenkins and Tanner (1968), Fisher and Tanner (1970), Nash and Tanner (1970), Avery and Tanner (1971), Rieppel (1981), and others. For the remainder of this discussion we will use the hyoid nomenclature followed by Romer (1956) as described earlier. The hyoids of the geckos *Coleonyx, Gekko, Aristelliger, Hemidactylus, Phyllodactylus, Thecadactylus*, and *Eublepharis* have been described, and we figure *Tarentola* (Fig. 4) and *Coleonyx* (Fig. 5). In most, the body of the hyoid is small and slender, with a long rodlike lingual process extending anteriorly. A pair of hyoid cornua extend laterally; in

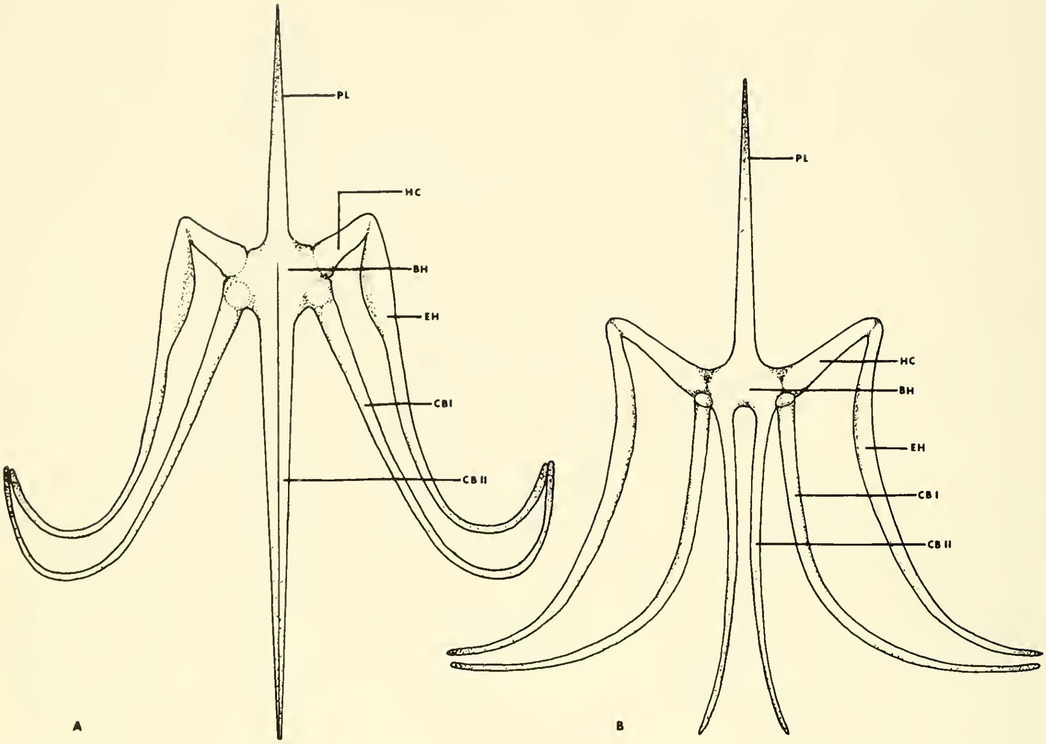


Fig. 6. Hyoid apparatus, ventral views: A, *Brachylophus brevicephalus* (BYU 32663); B, *Sauromalus obesus* (BYU 21728).

some species these form sigmoid curves, and in others they are straight rods. Articulating with the distal extremes of the hyoid cornua are the epihyals. Extending posteriorly from the body of the hyoid as a pair of short or long rods are the second ceratobranchials. A third set of arches, the first ceratobranchials, articulate at the point of attachment between the hyoid cornua and the body. The basic pattern is retained throughout the Gekkota, with some variation in the shape of the hyoid cornua; also, the first ceratobranchials, epihyals, or both may be lost in some genera.

In the Dibamidae, Rieppel (1981) has described the hyoid of *Dibamus* as having a posteriorly bifurcated basihyal with an elongated entoglossal process. The bony first ceratobranchials that articulate with the posterolateral limbs of the basihyal are shorter in *Dibamus* as compared to *Anniella*. He indicates a major specialization exists in that there are a pair of cartilaginous rods that support the aditus laryngis and approach but do not fuse to the posterolateral limbs of the basihyal. These he considers to be hypohyals (hyoid cornua of Romer).

The hyoids of the iguanine lizards *Amblyrhynchus, Brachylophus, Conolophus, Ctenosaura, Cyclura, Dipsosaurus, Iguana,* and *Sauromalus* and Malagashe iguanids *Chalarodon* and *Oplurus* have been investigated by Avery and Tanner (1971). Because these lizards possess all three arches of the hyoid apparatus, they are considered primitive (Fig. 6-A). The body of the hyoid (basihyal) is triangular in all the above genera except *Oplurus* and *Sauromalus,* in which it forms a broad flattened sheet of cartilage. In all the genera the hyoid cornu (hypohyal) is short and stout; it extends out from the body of the hyoid at right angles or projects slightly anterior to the body. Posterior to the body, the second ceratobranchials extend along the trachea and, in all genera except *Oplurus* and *Sauromalus,* lie close together. In the latter two genera the second ceratobranchials are widely separated by the bulk of the trachea (Fig. 6-B). In none of the genera are the sec-

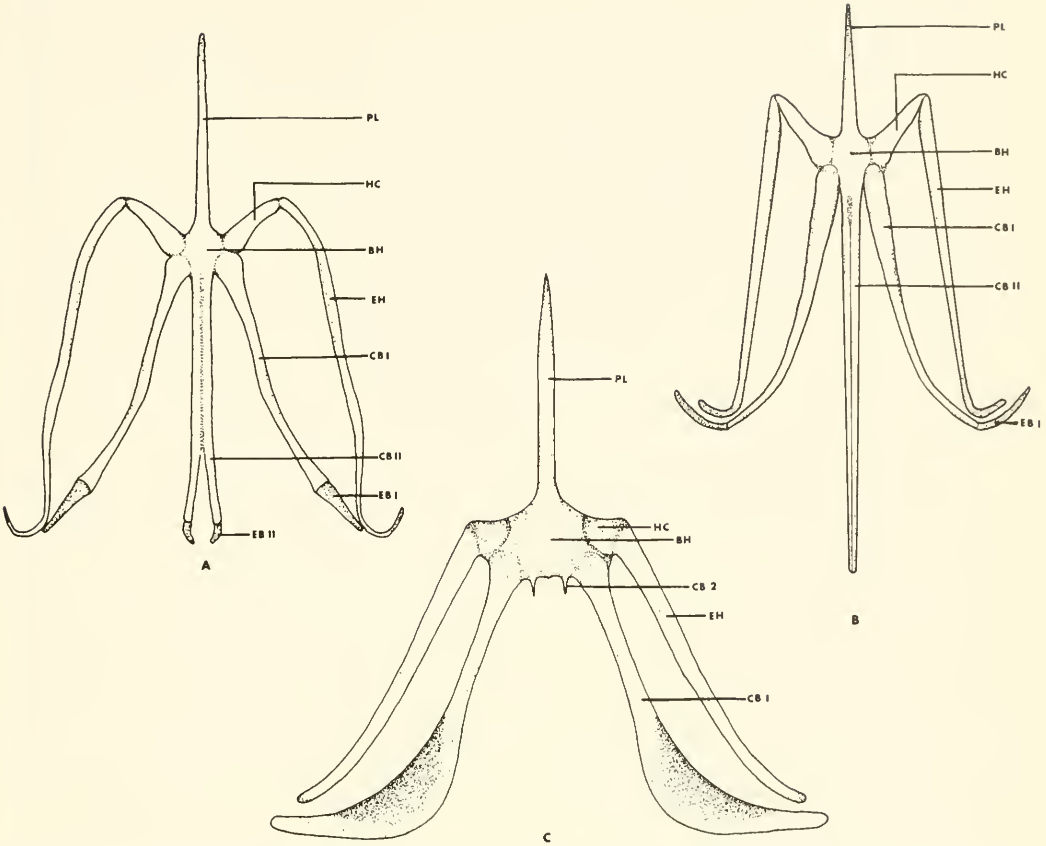


Fig. 7. Hyoid apparatus, ventral views: A, *Sceloporus magister* (BYU 30310); B, *Holbrookia maculata* (BYU 15752); C, *Phrynosoma platyrhinos* (BYU 22830).

ond ceratobranchials attached distally to the other arches. In some genera, particularly *Iguana*, the distal extremes of these processes attach to the skin and provide support for movement of the dewlap.

The first ceratobranchials articulate proximally with the body of the hyoid between the origins of the second ceratobranchials and the hyoid cornua. They are elongated, thin rods that taper to points distally and curve dorsolaterally to the sides of the neck, where they articulate with the epihyals (certohyals). The epihyals articulate between the hyoid cornua and the first ceratobranchials and form the most lateral extensions of the hyoid apparatus. At their proximal ends the epihyals are expanded into bladelike processes that extend medially toward the hyoid body. These processes are not developed to any degree in *Chalarodon* and *Oplurus*. Among the other iguanids studied and described by one of us are the hyoids of *Crotaphytus*, *Holbrookia*, *Phrynosoma*, and *Uta*. We figure *Sceloporus magister* and *Holbrookia maculata* (Figs. 7-A & B) as representatives of the sceloporine genera. The basic pattern described in the iguanines is maintained with the following exceptions. In *Phrynosoma* the second ceratobranchials are greatly reduced, and the first ceratobranchials and epihyals are noticeably thickened (Fig. 7-C); the basihyoid is a laterally extended plate. *Anolis* has an exceptionally elongated hyoid apparatus, with the second ceratobranchials extending posteriorly along the midline forming approximately two-thirds the length of the entire hyoid apparatus. This anatomical development is associated with the functional dewlap (Fig. 8).

In the agamids, the following were examined: *Agama* (Duda 1965, Hass 1973), and Figure 9; *Calotes*, *Draco*, and *Sitana* (Gnanamuthu 1937), *Chlamydosaurus* (Beddard 1905, DeVis 1883), *Phrynocephalus* (Haas 1973), *Physignathus* (Kesteven 1944), and *Uromastyx* (Poglayen-Neuwall 1954, Versluys 1898, El Toubi 1947b, Tilak 1964b). In general, the agamid hyoids resemble closely those of the iguanids. In *Uromastyx* the basihyoid is slender and laterally extended; the hyoid cornua are directed anterolaterally (Tilak 1964b). The short and widely separated second ceratobranchials extend posteriorly from the basihyoid. The first ceratobranchials extend posteriorly from the basihyoid. The first ceratobranchials articulate at the union of the hyoid cornua and the basihyoid. They comprise the longest elements of the hyoid. The epihyals attach to the distal ends of the hyoid cornua and have, at their distal ends, epibranchials that may attach to the distal end of the first ceratobranchials. In *Agama* (Fig. 9) the hyoid is similar except that the basihyoid is more massive and the second ceratobranchials are aligned more closely together. In *Calotes* and *Draco* the hyoids are elongated and narrow. The second ceratobranchials are exceptionally long and slender, lying close together at the midline, whereas

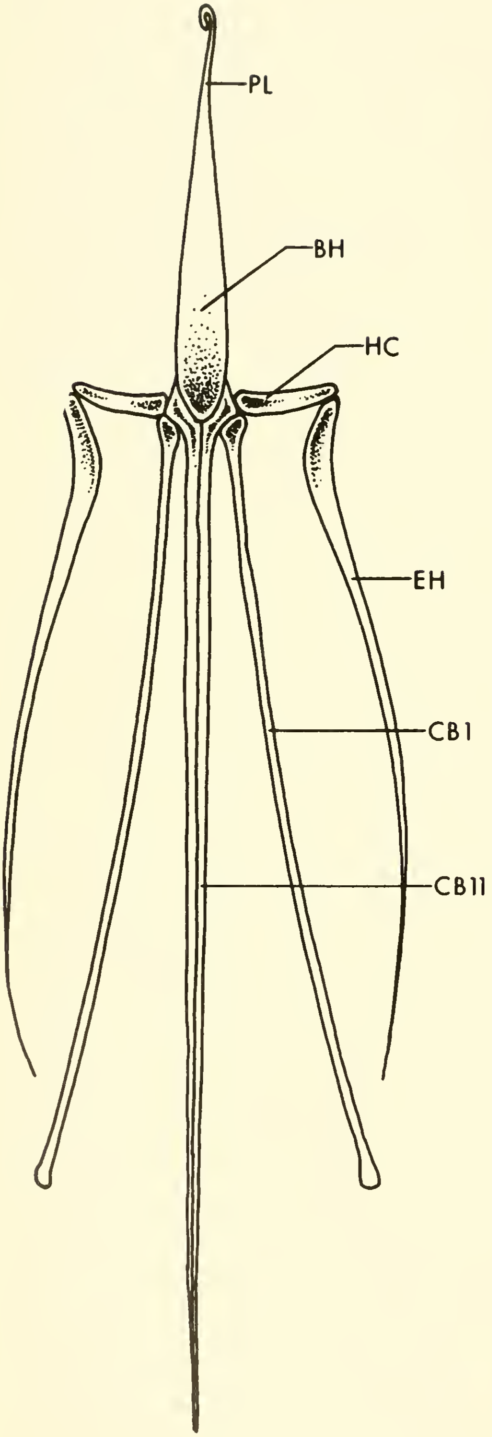


Fig. 8. Hyoid apparatus, ventral view: *Anolis carolinensis* (BYU 13768).

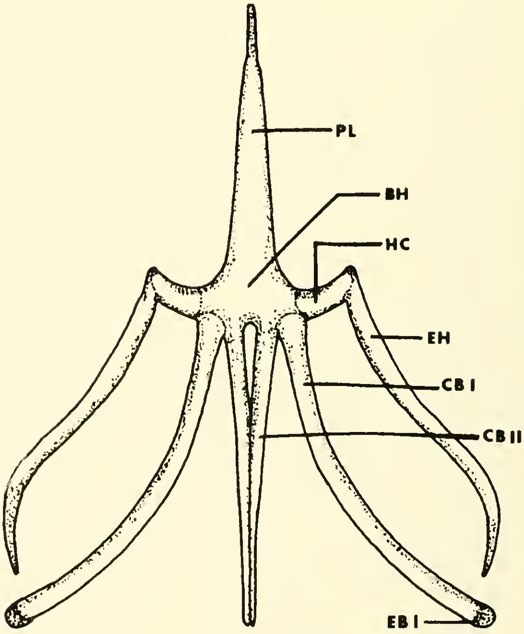


Fig. 9. Hyoid apparatus of *Agama agama* (BYU 18147), ventral view.

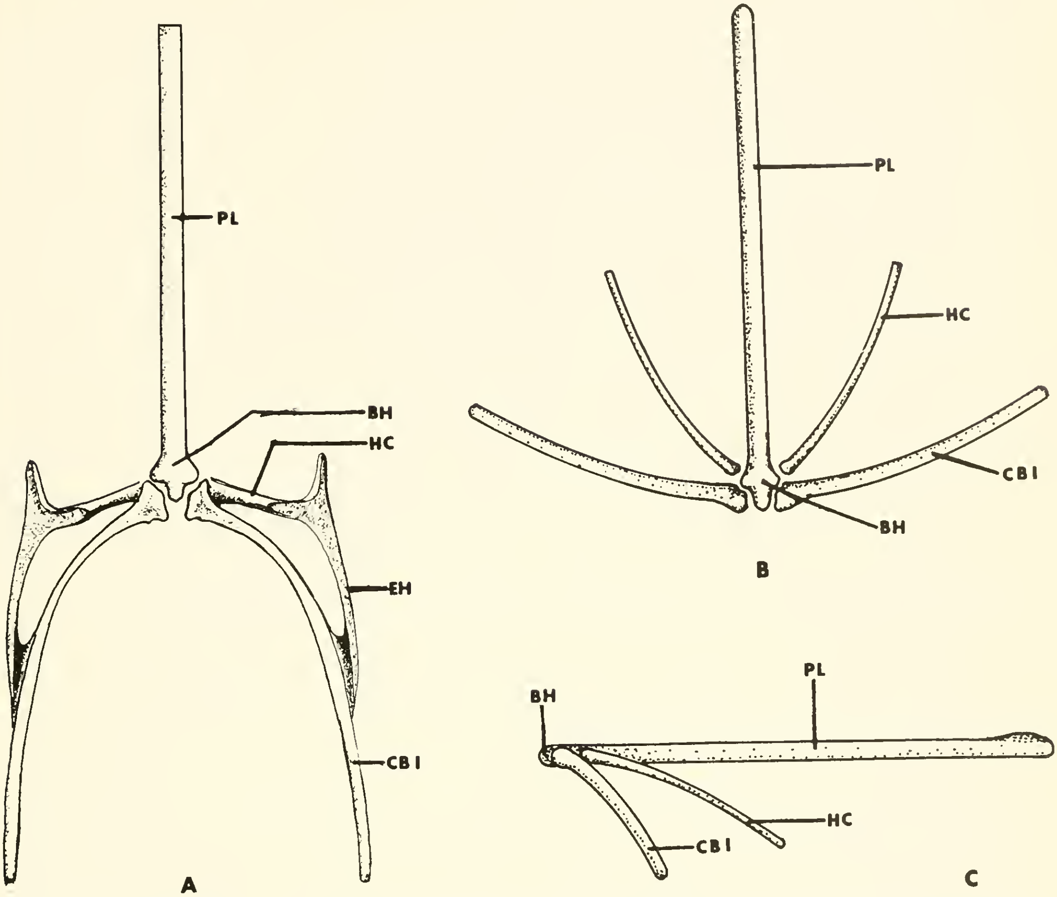


Fig. 10. Hyoid apparatus: A, *Chamaeleon namagyensis* (USNM 161275); B, *Chamaeleon brevicornis* (BYU 12422), ventral views; C, same as B, lateral view.

the epihyals are very short and not connected by epibranchials. In *Chlamydosaurus* the basihyoid is massive and bears two hornlike projections; these extend laterally to articulate with the hyoid cornua, which form short tapering tips on these projections. The second ceratobranchials appear to have been lost unless they are represented by two very small knobs on the posteromedial border of the basihyoid. The first ceratobranchials are extremely elongated, extending posterolaterally and composed of two pieces. The very long proximal piece articulates distally with the second piece, which is about one-fifth the length of the proximal. The epihyals are short or slender, and articulate at the point where the hyoid cornua and the lateral projections of the basihyoid attach. In *Physignathus* the hyoid exhibits a normal structure except that the first ceratobranchials are much longer than the second ceratobranchials.

In *Chamaeleo* the hyoid is distinctly different, with the basihyoid being little more than the basal part of the lingual process. The hyoid cornua extend anterolaterally about a third the length of the lingual process. The first ceratobranchials extend laterally and are short. The epihyals are small and attach to the hyoid cornua about half the distance from their distal ends. The second ceratobranchials are lost (Fig. 10-A, B, and C). Gnanamuthu (1937) described the hyoid apparatus for *Chamaeleo carcaratus* and reviewed previous studies of its function.

In the Scincidae the hyoids of *Scincus* (El Toubi 1938), *Eumeces* (Nash and Tanner 1970), Fig. 11, *Mabuya* (Richter 1933), and

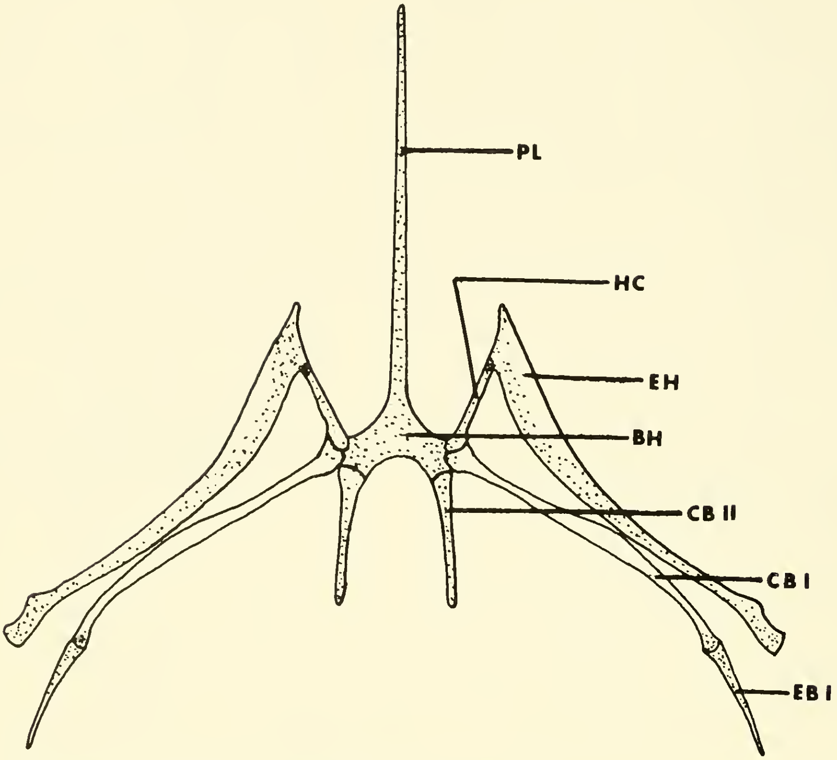


Fig. 11. Hyoid apparatus of *Eumeces gilberti* (BYU 31956), dorsal view. (After Nash and Tanner 1970)

Chalcides (Furbringer 1922, Richter 1933) have been described. All three arches are present and assume an unspecialized pattern. In all the basihyoid is broad rather than narrow, and the second ceratobranchials are very short and widely separated. The first ceratobranchials are elongate and slim. The hyoid cornua are short and slim, and articulate distally with the epihyals, which vary in form. They are simple rods in *Eumeces* and have enlarged proximal ends in the remaining genera. In *Scincus* the enlarged ends are simple and spoonshaped, but in *Chalcides* and *Mabuya* the shape is complex. In both genera the enlarged end has a short flange extending posterolaterally from the middle of the epihyal where the enlarged end terminates. These genera have a large hooklike second epibranchial associated with the distal end of the epihyal. It is attached in *Chalcides* and *Scincus* but separate in *Eumeces* and *Mabuya*. In all genera there is a short first epibranchial attached to the terminal end of the first ceratobranchial (Fig. 11).

Rieppel (1981) has examined the limbless scincoid genera *Acontias, Typhlosaurus,* and *Acontaphiops. Acontias* is described as being like *Anniella,* with the basihyal having a slender entoglossal process and being bifurcated posteriorly with its distinct posterolateral limbs articulating with first ceratobranchials. Hypohyal processes (hyoid cornua) are present in all species where they are T-shaped at their distal ends. In *Typhlosaurus* the hyoid is similar to *Acontias,* but the posterior first ceratobranchials are longer and hypohyals are absent. Rieppel calls attention to the fact that the hyoid of *Typhlosaurus* is identical to that of some Typhlopidae as described by List (1966) and Langebartel (1968). The hyoid of *Acontophiops* is similar to that of *Typhlosaurus.*

In the teiid *Tupinambis,* the lingual process is detached from the basihyoid and embedded in the tongue. The second ceratobranchials are lost, and the epihyals and first ceratobranchials are connected by epibranchials.

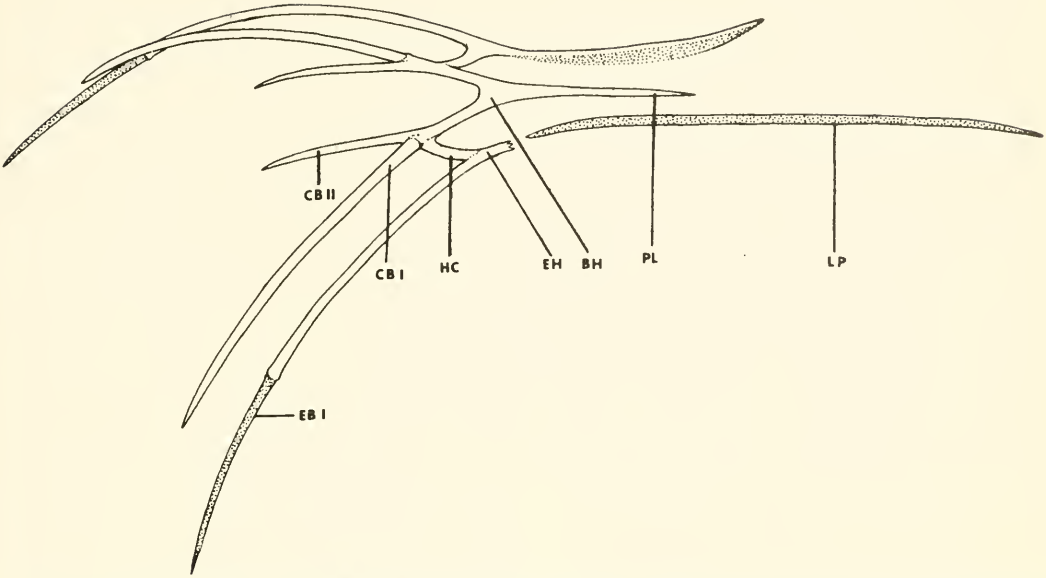


Fig. 12. Hyoid apparatus of *Cnemidophorus tigris* (BYU 31925). Dorsolateral view showing the detached lingual process (LP) and the extension of the body of the hyoid anteriorly as a spine.

The lingual process is also detached in *Cnemidophorus* (Fig. 12). The hyoid extends anteriorly as a short spine similar to that of iguanids except for its smaller size. It is embedded in connective tissue ventral to the lingual process and the tongue. The hyoid cornua extend anterolaterally from the basihyoid and articulate with the epihyals. The latter extend anteriorly, forming bladelike cartilages that serve as lateral supports for the posterior half of the tongue and extend laterally to lie adjacent to the mandible. The posterior part of the epihyal extends posteriorly, curving laterally where it terminates as cartilage in loose connective tissue on the first ceratobranchial. Both ceratobranchials are present; the first extends posteriorly to terminate in the connective tissue with the cartilagenous first epibranchial. The epihyals and first ceratobranchials are not connected distally, although the ends are close together in a common connective tissue.

Ameiva lacks the second ceratobranchials. The first epibranchials are short, forming a knob on the end of the ceratobranchials.

In both *Ameiva* and *Cnemidophorus* the detached lingual process extends anteriorly to approximately the forking of the tongue. Posteriorly it is tightly enclosed in connective tissue between the elongate M. hypoglossus. It terminates posteriorly, ventral to the laryngeal cartilages.

In *Anguis* (Anguidae) the hyoid is greatly reduced, with the second ceratobranchials and epihyals absent. The hyoid cornua are enlarged and extend anteriorly to parallel the lingual process for most of its length. In *Gerrhonotus* and *Ophisaurus* the second ceratobranchials are also lost. The epihyals are present, however, and articulate with the distal ends of the hyoid cornua, which are more laterally directed than in *Anguis*.

In *Varanus* (Varanidae), the hyoid cornua is complex and is composed of two articulating cartilaginous rods, called by Sondhi (1958:159–160) the portio proximalis (hyoid cornu) and the portio distalis (epihyal):

> Each has an anterior handlelike process and in life the two hooked ends cross each other beneath the tongue-sheath, with the handle of the portio proximalis lying dorsal to that of the portio distalis.

According to Sondhi (1958:159–160),

> the proximal end of the portio proximalis fits into a roughly concave facet on the dorsolateral surface of the basihyoid, near the facet at which the posterior cornua articulates. From this point the portio proximalis extends obliquely upward, outward, and forward and at its termination curves inward to form the hook-shaped handle that is dorsoventrally flattened. The portio distalis is flattened at its proximal handlelike end, becomes rodlike as it passes backward and upward, and gradually

> tapers at its distal end. It is disposed obliquely across the sides of the neck, its tapering end lying almost parallel to the proximal piece of the posterior cornua of its side.

Sondhi also indicates that the portio proximalis and portio distalis are attached to each other by a cartilaginous piece, with this attaching piece being folded at its outer margin like a cover of a folder so that one part of it becomes dorsal and the other ventral. The dorsal part is described as

> narrower and is attached to the flattened, curved anterior end of the portio proximalis like the blades of scissors on its counterpart. The nature of attachment of the two pieces of the anterior cornua renders them capable of opening out to some extent like the covers of a folder.

The description of *V. monitor* (Sondhi 1958) and our dissection of *V. indicus* (BYU 40944) differ somewhat. We did not find a cartilaginous connection between the portio proximals (hyoid cornu) and the portio distalis (epihyal). The only attachment is a lateral sheet of connective tissue that provides a loose connection. The expanded ends are not connected medially and are, therefore, folded as two separate sheets. Near the middle of the epihyal of *V. indicus*, a thin lateral expansion of cartilage is connected by a sheet of connective tissue to the lateral edge of the hyoid cornu. The distal end of the hyoid cornu is slightly flattened, but not expanded (Fig. 13).

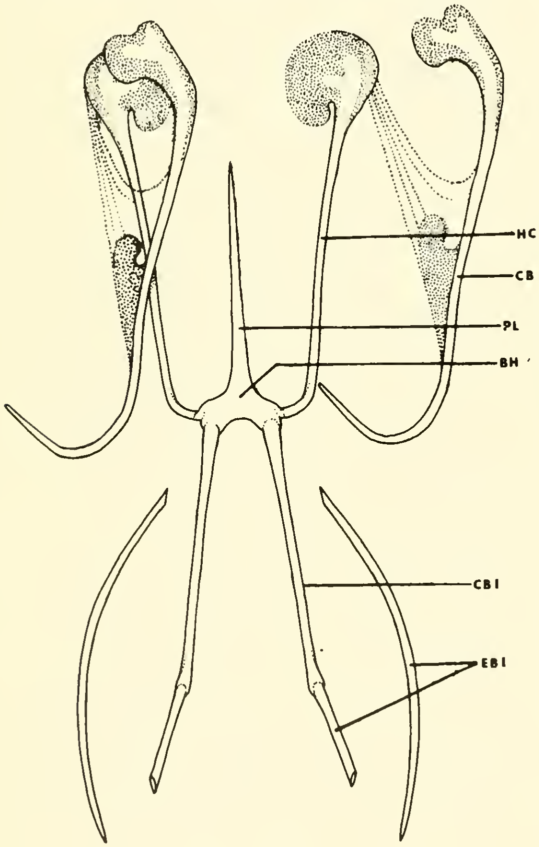


Fig. 13. Hyoid apparatus of *Varanus indicus* (BYU 40944). Ventral view with the left epihyal reflected to show the absence of a cartilage connection between it and the distal end of the hyoid cornu. Dotted lines extending from the cartilaginous median part of the epihyal represents connective tissue. The elongate first epibranchials are cut.

The lingual process is shorter than that of *V. monitor* as figured by Sondhi, and does not extend anterior to the level of the expanded anterior ends of the hyoid cornu and the epihyal. In *Varanus* the first ceratobranchial and first epibranchial are greatly elongated, and the latter taper to a small rod terminating in connective tissue anterodorsal to the shoulder.

In *Heloderma* the second ceratobranchials are lost, and the epihyal is continuous with the hyoid cornu, forming a sigmoid curve. A joint exists at their point of articulation. The first ceratobranchials are also curved and diverge far laterally at their distal ends. In *Xenosaurus* as well, the second ceratobranchials are lost, but the epihyals are straight and long, with a hook at their distal end. The area of articulation between the epihyal and hyoid cornu is enlarged to form a knob. The hyoid cornua extend anterolaterally about two-thirds the length of the lingual process. McDowell and Bogert (1954) report that the hyoids of *Lanthanotus* and *Heloderma* are basically similar except *Lanthanotus* has lost the epihyals. Rieppel (1981) investigated *Lanthanotus* and found hypohyals (epihyal of McDowell and Bogert) that were reported absent by McDowell and Bogert (1954), although McDowell (1972:213) later did report them to be present. Rieppel rejects the argument of McDowell and Bogert that *Lanthanotus* is close to the origin of snakes. Rieppel (1981:435) states,

> neither the shape of the basihyal nor any other feature of the hyobranchial skeleton of *Lanthanotus* shows a particular similarity to the ophidian hyoid.

Through the courtesy of Dr. Richard Zweifel we were privileged to examine the throat

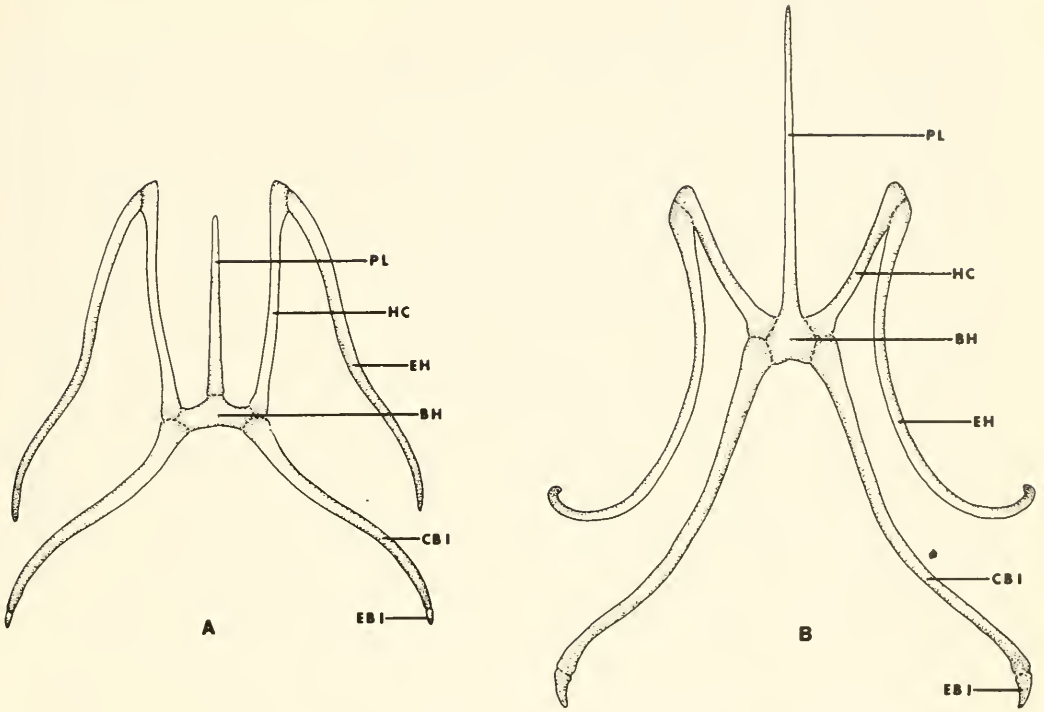


Fig. 14. Hyoid apparatus, ventral views: A, *Lanthanotus borneensis* (AMNH 87375); B, *Heloderma suspectum* (BYU 41436).

anatomy of *Lanthanotus boreensis* (AMNH 87375) and found the hyoid skeleton to be surprisingly similar to that of *Heloderma* (Fig. 14). Rieppel (1980, 1981) has, on the basis of cranial anatomy, concluded that *Lanthanotus* is intermediate in structure between *Heloderma* and *Varanus*. Branch (1982) arrived at a similar conclusion based on hemipeneal data. The hyoid of these genera have the same structures; however, in *Varanus* there has been considerable modification and specialization not found in the other genera.

In *Gerrhosaurus* (Cordylidae) the second ceratobranchials have been lost, but the first ceratobranchial and epihyal are retained. In *Zonurus* the second ceratobranchials are present but short. In *Xantusia* (Xantusidae) the hyoid contains all the elements. The hyoid cornu extends dorsolaterally to articulate with the median edge of the expanded, flattened proximal end of the epihyal. From the flattened end the epihyal extends posterodorsally, tapering into a rod and terminating as a short epibranchial immediately posterior to the tympanum. The first ceratobranchial extends posterodorsally and curves to terminate in the second epibranchial and in close association with the epibranchial of the epihyal.

The second ceratobranchial in *Xantusia* extends posterior with the distal end, curving laterad to form an open hook. It does not articulate with an epibranchial as in the epihyal and first ceratobranchial; however, a cartilaginous structure in close association with the distal end of the second ceratobranchial extends laterally and curves anteriorly to articulate with the basioccipital of the skull. Cope (1900) and Savage (1963) have referred to this structure as a free epibranchial. If this is an epibranchial, it is distinct and differs from all others in saurians we have seen. Its close association to the distal end of the second ceratobranchial (Fig. 15) is not articulated as in the other epibranchials and leads us to believe that the entire structure may represent fusions of other remnant gill bars. An examination of the entire structure (Fig. 15B) indicates to us that fusions have occurred. An articulation or close association of the distal ends of the epihyal and/or the second ceratobranchial occurs in many forms

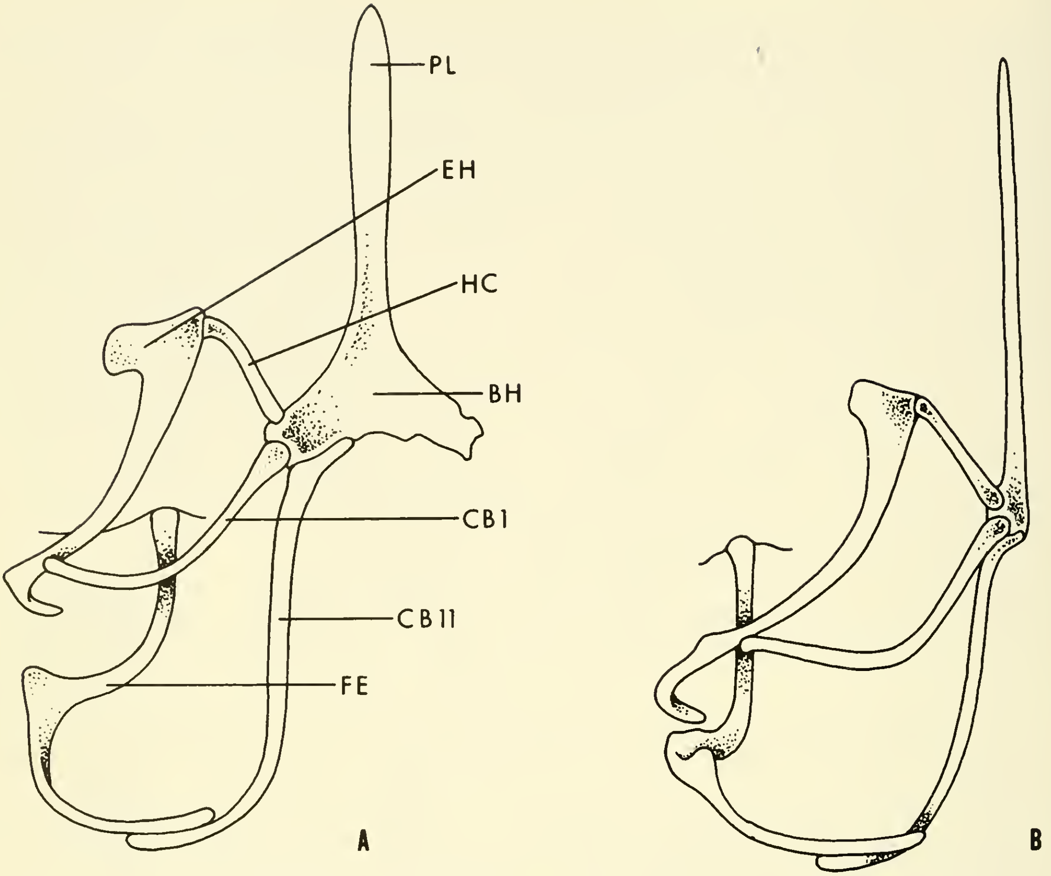


Fig. 15. Hyoid apparatus of *Xantusia vigilis* (BYU 21765): A, ventral view; B, lateral view. (FE = "free epibranchial")

but the "free epibranchial" is unique to the xantusids.

The hyoid of *Anniella* has been described by Cope (1892) and Rieppel (1981). According to Rieppel, the basihyal is bifurcated posteriorly and bears a long entoglossal process. It articulates posteriorly with first ceratobranchials, and small hyohyals (hyoid cornua) are present. These latter structures were considered absent by Cope and Langebartel (1968).

In *Amphisbaenia* all the elements are present, with the second ceratobranchials being short and widely separated. The hyoid cornu extends anterolaterally, with its distal end free. The epihyal articulates with the cornu about one quarter of its distance from the proximal end. The first ceratobranchial articulates at the point of articulation between the hyoid cornu and the body of the hyoid. Its terminal end bears an epibranchial. All the posterior projections of the hyoid extend straight back and remain unattached at their distal ends (Fig. 16).

Ophidia

The hyoids of snakes have been extensively discussed by Langebartel (1968) and others as follows:

Anomalepididae
  Anomalepis (Smith and Warner 1948), *Helminthophis* (List 1966, Langebartel 1968), *Liotyphlops* (List 1966, Langebartel 1968).

Typhlopidae
  Typhlophis (Evans 1955, List 1966), *Typhlops* (List 1966, Langebartel 1968).

Leptotyphlopidae
  Leptotyphlops (Smith and Warner 1948, List 1966, Langebartel 1968, Oldham, Smith, and Miller 1970).

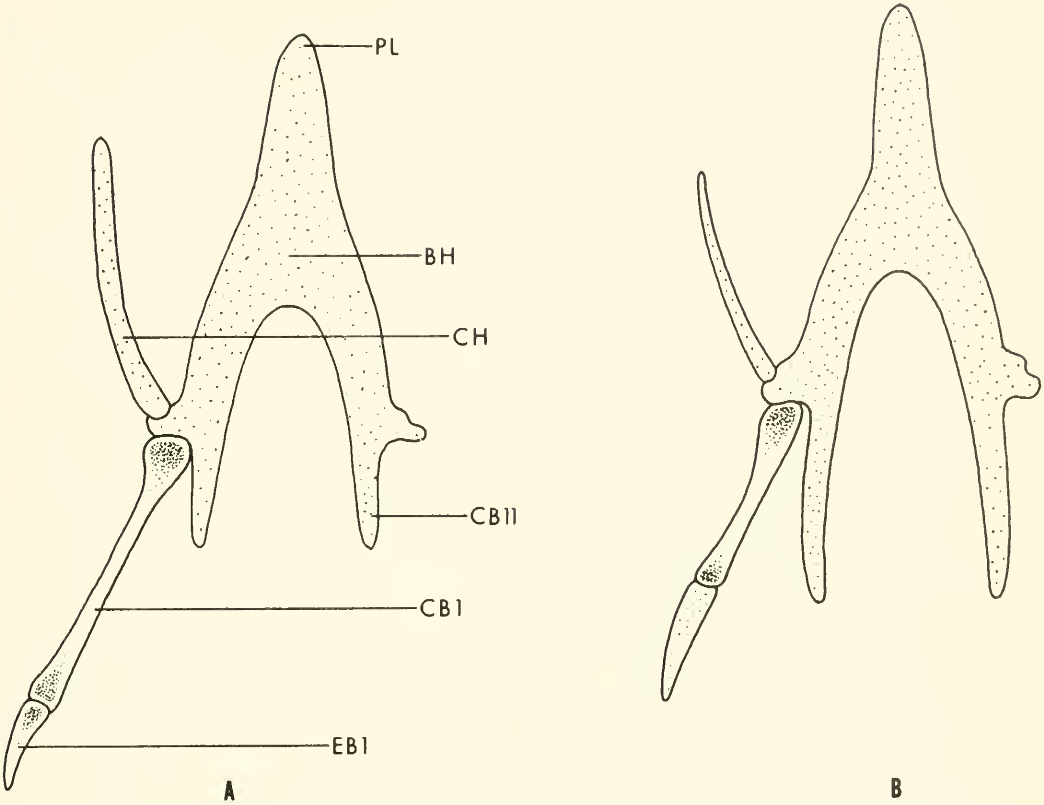


Fig. 16. Hyoid apparatus, ventral views: A, *Amphisbaenia cornura* (BYU 16127); B, *Amphisbaenia kingi* (BYU 16148).

Uropeltidae

Platyplactrurus (Langebartel 1968), *Plectrurus* (Rieppel 1981), *Rhinophis* (Smith and Warner 1948, Langebartel 1968), *Silybura* (Langebartel 1968).

Aniliidae

Anilius (Smith and Warner 1948, Langebartel 1968, Rieppel 1981), *Cylindrophis* (Smith and Warner 1948, Langebartel 1968).

Xenopeltidae

Xenopeltis (Smith and Warner 1948, Langebartel 1968).

Boidae

Aspidites (Smith and Warner 1948, Langebartel 1968), *Boa* (Langebartel 1968), *Calabaria* (Langebartel 1968), *Charina* (Langebartel 1968), *Chondropython* (Langebartel 1968), *Constrictor* (Langebartel 1968), *Enygrus* (Langebartel 1968), *Epicrates* (Langebartel 1968), *Liasis* (Langebartel 1968), *Lichanura* (Langebartel 1968), *Loxocemus* (Smith and Warner 1948, Langebartel 1968), *Nardoana* (Langebartel 1968), *Python* (Furbringer 1922, Langebartel 1968, Oldham, Smith, and Miller 1970), *Sanzinia* (Langebartel 1968), *Trachyboa* (Langebartel 1968).

Colubridae

Achalinus (Langebartel 1968), *Achrochordus* (Smith and Warner 1948, Langebartel 1968), *Adelphicus* (Langebartel 1968), *Amblycephalus* (Smith and Warner 1948, Langebartel 1968), *Aparallactus* (Langebartel 1968), *Apostolepis* (Langebartel 1968), *Atretium* (Langebartel 1968), *Boiga* (Langebartel 1968), *Carphophis* (Smith and Warner 1948, Langebartel 1968), *Cerberus* (Langebartel 1968), *Chersodromus* (Langebartel 1968), *Chersydrus* (Langebartel 1968), *Chrysopelea*

(Langebartel 1968), *Clelia* (Langebartel 1968), *Coluber* (Walter 1887, Langebartel 1968), *Coniophanes* (Langebartel 1968), *Conophis* (Langebartel 1968), *Conopsis* (Langebartel 1968), *Crotaphopeltis* (Langebartel 1968), *Cyclagras* (Langebartel 1968), *Dasypeltis* (Smith and Warner 1948, Langebartel 1968), *Dendrophidion* (Langebartel 1968), *Diadophis* (Langebartel 1968), *Dipsadoboa* (Langebartel 1968), *Dispholidus* (Langebartel 1968), *Dromophis* (Langebartel 1968), *Drymarchon* (Langebartel 1968), *Drymobius* (Langebartel 1968), *Dryophis* (Langebartel 1968), *Elaphe* (Langebartel 1968), *Elapomorphus* (Langebartel 1968), *Elapops* (Langebartel 1968), *Enhydrus* (Langebartel 1968), *Enulius* (Langebartel 1968), *Farancia* (Langebartel 1968), *Ficimia* (Langebartel 1968), *Fimbrios* (Langebartel 1968), *Geophis* (Langebartel 1968), *Haldea* (Langebartel 1968), *Haplopeltura* (Langebartel 1968), *Heterodon* (Weaver, 1965, Langebartel 1968), *Homalopsis* (Langebartel 1968), *Lampropeltis* (Langebartel 1968), *Leptodeira* (Langebartel 1968), *Leptophis* (Langebartel 1968), *Manolepis* (Langebartel 1968), *Masticophis* (Langebartel 1968), *Mehelya* (Langebartel 1968), *Natrix* (Sondhi 1958), *Nerodia* (Langebartel 1968, Oldham, Smith, and Miller 1970), *Ninia* (Langebartel 1968), *Nothopsis* (Langebartel 1968), *Opheodrys* (Langebartel 1968, Cundall 1974), *Oxybelis* (Langebartel 1968), *Oxyrhabdinium* (Langebartel 1968), *Pituophis* (Smith and Warner 1948, Bullock and Tanner 1966, Langebartel 1968, Oldham, Smith, and Miller 1970), *Psamaodynastes* (Langebartel 1968), *Rhadineae* (Langebartel 1968), *Rhadinella* (Langebartel 1968), *Rhinocheilus* (Langebartel 1968), *Salvadora* (Langebartel 1968), *Sibynomorphus* (Langebartel 1968), *Sibynophis* (Langebartel 1968), *Sonora* (Langebartel 1968), *Tantilla* (Langebartel 1968), *Thamnophis* (Bullock and Tanner 1966, Langebartel 1968, Oldham, Smith, and Miller 1970), *Toluca* (Langebartel 1968), *Trimorphodon* (Langebartel 1968), *Tropidonotus* (Langebartel 1968), *Xenodermus* (Langebartel 1968), *Xenodon* (Weaver 1965).

Elapidae

Acanthophis (Langebartel 1968), *Aspidelaps* (Langebartel 1968), *Bungarus* (Langebartel 1968), *Calliophis* (Langebartel 1968), *Demansia* (Langebartel 1968), *Dendraspis* (Langebartel 1968), *Denisonia* (Langebartel 1968), *Doliophis* (Langebartel 1968), *Elaps* (Langebartel 1968), *Elapsoidea* (Langebartel 1968), *Furina* (Langebartel 1968), *Hemachatus* (Langebartel 1968), *Hemibungarus* (Langebartel 1968), *Leptomicrurus* (Langebartel 1968), *Maticora* (Langebartel 1968), *Micruroides* (Langebartel 1968), *Micrurus* (Smith and Warner 1968, Langebartel 1968), *Naja* (Langebartel 1968, Kamal, Hamouda, and Mokhtar 1970), *Notechis* (Langebartel 1968), *Ogmodon* (Langebartel 1968), *Pseudelaps* (Langebartel 1968), *Ultocalamus* (Langebartel 1968).

Eydrophidae

Aipysurus (Langebartel 1968), *Hydrophis* (Langebartel 1968), *Kerilia* (Langebartel 1968), *Lapemis* (Smith and Warner 1948, Langebartel 1968), *Laticauda* (Langebartel 1968), *Thalasophina* (Langebartel 1968).

Viperidae

Aspis (Langebartel 1968), *Atheris* (Langebartel 1968), *Atractaspis* (Langebartel 1968), *Bitis* (Langebartel 1968), *Causus* (Langebartel 1968), *Cerastes* (Langebartel 1968), *Echis* (Langebartel 1968), *Pseudocerastes* (Langebartel 1968), *Vipera* (Langebartel 1968, Furbringer 1922).

Crotalidae

Agkistrodon (Smith and Warner 1948, Langebartel 1968), *Bothrops* (Langebartel 1968), *Crotalus* (Langebartel 1968, Oldham, Smith, and Miller 1970), *Lachesis* (Langebartel 1968), *Sistrurus* (Langebartel 1968), *Trimeresurus* (Langebartel 1968).

In snakes the hyoid apparatus is greatly reduced, with the hyoid cornua being lost and the remainder of the processes simplified. Essentially the snake hyoid consists of a body plus a lingual process and what is thought to be the second ceratobranchials, which are fused to the body of the hyoid (Figs. 17A and B, 29). The variations found in ophidian hyoids have been discussed by Furbringer

(1922), Versluys (1936), Gnanamuthu (1937), Smith and Warner (1948), Sondhi (1958), Albright and Nelson (1959), List (1966), Underwood (1967), Langebartel (1968), Rieppel (1981), and others. There are four major morphological types that can be distinguished in snakes. These correspond in shape roughly to the letters M, Y, and V, and to a parallel type 11. The most complete survey of the hyoids of snakes is presented by Langebartel (1968), and we have based much of our remarks on his study.

Hyoids possessing the M shape are found exclusively in the family Anomalepididae, which has only four genera, *Anomalepis, Liotyphlops, Helminthophis,* and *Typhlophis.* In this group the hyoid has a body and the second ceratobranchials. All other processes are lost, including the lingual process.

A Y-shaped hyoid is found in the Typlopidae and Leptotyphiopidae. The body of the hyoid possesses a lingual process and has hyoid cornua (second ceratobranchials) that project posteriorly. The possession of a lingual process is variable, with it being absent according to List (1966) in *Typhlops pusillus* and *T. lumbricalis.* In *T. reticulatus, T. platycephalus,* and *T. blandfordi lestradei* the hyoid cornua are separated from the body. *Leptotyphlops* has a normal Y type hyoid.

The V-shaped hyoid is found in the Aniliidae, Boidae, Uropeltidae, and Zenopeltidae. In this type of hyoid the lingual process is absent and the hyoid cornua may be attached or unattached. There is much intraspecific variation in the latter character. In some specimens of *Charina bottae* the cornua are attached, although they are unattached in others. Langebartel (1968) considers the curving arches to be the first ceratobranchials.

The 11 type hyoid is found in the colubrids, crotalids, elapids, hydrophids, viperids, and some genera of the boidae (*Casarea, Trachyboa,* and *Tropilophis*). The second ceratobranchials of this type are usually long, parallel rods attached to a slim hyoid body (Fig. 17). The resulting structure resembles a tuning fork in appearance. A few snakes have a hyoid body, triradiate in appearance and with a short lingual process. Such a structure is figured by Sondhi (1958) for *Natrix* (*Xenochrophis*), in which:

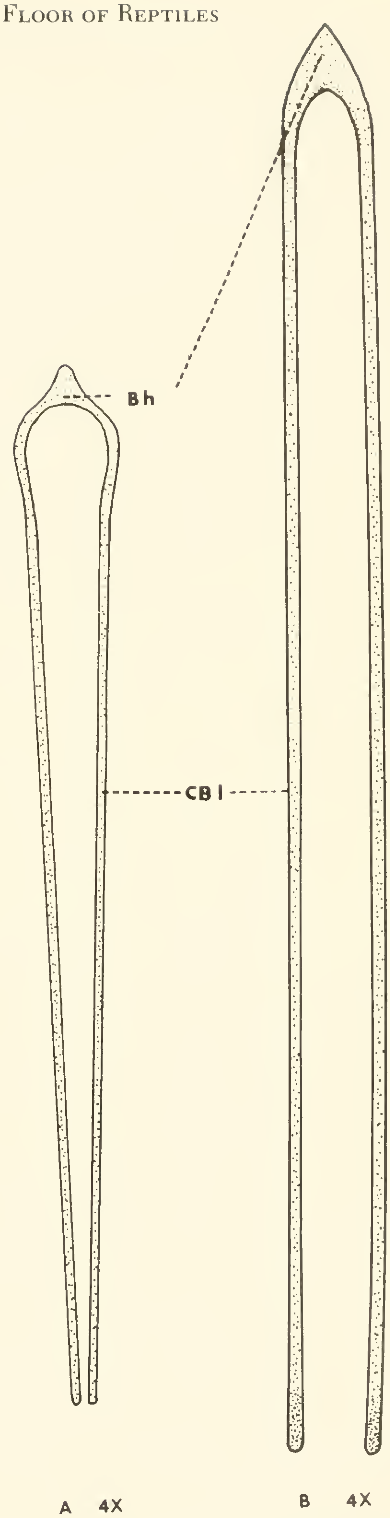


Fig. 17. Hyoid apparatus, ventral views: A, *Pituophis m. deserticola* (BYU 3072); B, *Crotalus viridis lutosus* (2089). Both are from adult individuals and drawn at 4X actual size.

the basihyoid lies ventral to the trachea and dorsal to the posterior terminations of the omohyoideus and sternohyoideus muscles.

The processes form elongated rods that lie ventral and extend posteriorly and parallel, with their terminal ends enclosed in the tips of the base of the tongue. In *Pituophis*, the basihyoid is ventral to the tongue at about the level of the angle of the jaws. The ceratobranchials extend and curve posterolaterally from the basihyoid for a short distance to a lateral position and then extend posteriorly, lateral to the tongue and parallel to each other, to the posterior tip of the tongue. In *Crotalus* the same obtains anteriorly with the basihyoid and the anterior part of the ceratobranchials; however, the posterior third of the latter converge ventrally to become closely associated along the ventromedian of the tongue and diverge slightly near their ends to become imbedded in muscle and connective tissue (Fig. 28, Romer 1950:fig. 421-C, Langebartel 1968:figs. 3, 4). For detailed description of the hyoid of individual genera of snakes, see Langebartel (1968).

III. Muscles of the Buccal Floor: General

The buccal floor is composed of several interwoven sheets of muscles. These sheets can be separated into two major groups: the hypobranchial musculature and the muscles of the associated branchial arches. The hypobranchial muscles are derived from the myotomes of the occipital and cervical somites, whereas the muscles of the branchial arches come from the viceral muscle plates formed in the branchial region. The tongue, for the most part, is also derived from the occipital somites. Because of the close associations of some of the somites with both cranial and spinal areas, some muscles are innervated by both spinal and cranial nerves.

For the sake of convenience, we have separated our discussion of the buccal musculature into two major divisions: (1) the muscles associated with the hyoid apparatus and (2) those associated with other structures. The tongue is sufficiently important to be segregated from these categories and is considered under a separate heading.

The nomenclature of muscles of reptiles has not been standardized; however, tables of synonyms can be found in Edgeworth (1935), Langebartel (1968), Haas (1973), and Schumacher (1973). Some of the more recent short summaries of the earlier papers on the myology of the buccal floor in reptiles can be found in Sondhi (1958), Langebartel (1968), Avery and Tanner (1971), Secoy (1971), and Varkey (1979). The remainder of this section is a brief account of the musculature of the buccal floor in selected reptiles as described by several earlier workers such as Edgeworth (1931), Graper (1932), Gnanamuthu (1937), Reese (1915 and 1932), Hacker and Schumacher (1955), Oelrich (1956), Sondhi (1958), Langebartel (1968), and others. It also should be noted that the more advanced reptiles have more complex muscular patterns when compared to primitive forms. This is seemingly true not only for orders, but also for family groups. A comparison of the advanced lizard *Varanus* and the primitive iguanids in the following sections serves as an illustration.

We refer to such forms as *Gavialis*, *Trionyx*, *Natrix* (*Xenochrophis*), *Varanus*, and other genera. These should be credited to Gnanamuthu (1937) or Sondhi (1958) if not otherwise noted.

The musculature of the following reptiles has been studied.

Chelonia

Pelomedusidae
Pelusios (Poglayen-Neuwall 1953a).

Chelidae
Batrochemys (Poglayen-Neuwall 1953a), *Chelodina* (Poglayen-Neuwall 1953a).

Chelydridae
Chelydra (Camp 1923, Graper 1932, Poglayen-Neuwall 1953a, Schumacher (1973), *Kinosternon* (Poglayen-Neuwall 1953a, Schumacher 1973), *Sternotherus* (Poglayen-Neuwall 1953a, Schumacher 1973).

Testudinidae
Chrysemys (Poglayen-Neuwall 1953a, Ashley 1955, Schumacher 1973), *Cuora* (Poglayen-Neuwall 1953a), *Clemmys* (Graper 1932), Poglayen-Neuwall 1953a, Schumacher 1973), *Deirochelys* (Shah 1963), *Emys*

(Walter 1887, Schumacher 1973), *Gopherus* (George and Shad 1954), *Graptemys* (Poglayen-Neuwall 1953a), *Geochelone* (Bojanus 1819, Graper 1932, Lubosch 1933, Edgeworth 1935, Poglayen-Neuwall 1953a, George and Shad 1955, Schumacher 1973), *Malaclemys* (Poglayen-Neuwall 1953a), *Pseudemys* (Ashley 1955, Poglayen-Neuwall 1953a, Schumacher 1973), *Terrapene* (Poglayen-Neuwall 1953a).

Trionychidae

Lissemys (George and Shad 1954, Sondhi 1958, Schumacher 1973), *Trionyx* (Graper 1932, Lubosch 1933, Poglayen-Neuwall 1953a, Sondhi 1958, Schumacher 1973).

Cheloniidae

Caretta (Poglayen-Neuwall 1953a, Schumacher 1973).

Dermochelyidae

Dermochelys (Poglayen-Neuwall 1953a, 1953/54, Schumacher 1973).

Rhynchocephalia

Sphenodontidae

Sphenodon (Osawa 1898, Camp 1923, Byerly 1926, Lubosch 1933, Edgeworth 1935, Lightoller 1939, Kesteven 1944, Rieppel 1978).

Lacertilia

Gekkonidae

Coleonyx (Camp 1923), *Gekko* (Camp 1923, Lubosch 1933), *Gymnodactylus* (Brock 1938, Kesteven 1944), *Hemidactylus* (Zavattari 1908, Ping 1932, Edgeworth 1935, Gnanamuthu 1937), *Platydactylus* (Sanders 1870, Poglayen-Neuwall 1954), *Stenodactylus* (Camp 1923, Edgeworth 1935), *Tarentola* (Gnanamuthu 1937, Poglayen-Neuwall 1954), *Thecodactylus* (Kesteven 1944).

Dibamidae

Dibamua (Gasc 1968).

Iguanidae

Amblrhynchus (Avery and Tanner 1971), *Anolis* (Kesteven 1944), *Basiliscus* (Gnanamuthu 1937), *Brachylophus* (Camp 1923, Avery and Tanner 1971), *Callisaurus* (Cox and Tanner 1977), *Chalarodon* (Avery and Tanner 1971), *Conolophus* (Cox and Tanner 1977), *Crotaphytus* (Davis 1934, Robison and Tanner 1968), *Ctenosaura* (Oelrich 1956, Avery and Tanner 1971), *Cyclura* (Avery and Tanner 1971), *Dipsosaurus* (Avery and Tanner 1971), *Enyaliosaurus* (Avery and Tanner 1971), *Hol brookia* (Cox and Tanner 1977), *Iguana* (Mivart 1867, Edgeworth 1935, Poglayen-Neuwall 1954, Avery and Tanner 1971, Oldham and Smith 1975), *Oplurus* (Avery and Tanner 1971), *Phrynosoma* (Sanders 1874, Camp 1923, Jenkins and Tanner 1968), *Sauromalus* (Avery and Tanner 1964, 1971), *Sceloporus* (Secoy 1971), *Tropidurus* (Zavattari 1908, Edgeworth 1935), *Uma* (Cox and Tanner 1977), *Urosaurus* (Fanghella, Avery and Tanner 1975), *Uta* (Fanghella, Avery and Tanner 1975).

Agamidae

Agama (DeVis 1883, Lubosch 1933, Edgeworth 1935, Poglayen-Neuwall 1954, Harris 1963), *Amphibolurus* (Poglayen-Neuwall 1954), *Calotes* (Camp 1923, Gnanamuthu 1937, Poglayen-Neuwall 1954), *Chlamydosaurus* (DeVis 1883), *Draco* (Gnanamuthu 1937), *Leiolepis* (Sanders 1872, Poglayen-Neuwall 1954), *Phrynocephalus* (Kesteven 1944), *Physignathus* (Kesteven 1944), *Sitana* (Gnanamuthu 1937), *Uromastix* (Furbringer 1922, Kubosch 1933, Edgeworth 1935, George 1948, Poglayen-Neuwall 1954, Throckmorton 1978).

Chamaeleonidae

Chamaeleo (Mivart 1870, Zavattari 1908, Camp 1923, Lubosch 1933, Edgeworth 1935, Gnanamuthu 1937, Kesteven 1944, Poglayen-Neuwall 1954).

Scincidae

Eumeces (Zavattari 1908, Edgeworth 1935, Nash and Tanner 1970), *Mabuya* (Gnanamuthu 1937), *Tiliqua* (Lightoller 1934, Kesteven 1944, Poglayen-Neuwall 1954), *Trachysaurus* (Poglayen-Neuwall 1954).

Cordylidae

Cordylus (Camp 1923, Edgeworth 1935), *Gerrhosaurus* (Camp 1923).

Lacertidae

Cabrita (Gnanamuthu 1937), *Lacerta* (Walter 1887, Camp 1923, Edgeworth 1935, Poglayen-Neuwall 1954).

Teiidae

Ameiva (Poglayen-Neuwall 1954, Fisher and Tanner 1970), *Cnemidophorus* (Poglayen-Neuwall 1954, Fisher and Tanner 1970), *Tupinambis* (Zavattari 1908, Camp 1923, Edgeworth 1935, Poglayen-Neuwall 1954).

Anguinidae

Gerrhonotus (Camp 1923, Poglayen-Neuwall 1954), *Ophiosaurus* (Poglayen-Neuwall 1954).

Xenosauridae

Shinosaurus (Haas 1960), *Xenosaurus* (Camp 1923, Haas 1960).

Helodermatidae

Heloderma (Camp 1923, Poglayen-Neuwall 1954).

Varanidae

Varanus (Bradley 1903, Camp 1923, Edgeworth 1935, Gnanamuthu 1937, Lightoller 1939, Kesteven 1944, Poglayen-Neuwall 1954, Sondhi 1958).

Anniellidae

Anniella (Camp 1923).

Amphisbaenidae

Amphisbaena (Smalian 1885, Camp 1923), *Anopsibaena* (Smalian 1885). *Bipes* (Smalian 1885, Renous 1977), *Blanus* (Smalian 1885), *Rhineura* (Camp 1923), *Trogonophis* (Smalian 1885).

Xantusidae

Xantusia (Camp 1923).

Ophidia

Anomalopididae

Anomalepis (Haas 1968), *Helminthophis* (Langebartel 1968), *Liotyphlops* (Langebartel 1968).

Typhlopidae

Typhlophis (Evans 1955), *Typhlops* (Langebartel 1968).

Leptotyphlopidae

Leptotyphlops (Langebartel 1968, Oldham, Smith, and Miller 1970).

Uropeltidae

Platylectrurus (Langebartel 1968), *Rhinophis* (Langebartel 1968), *Uropeltis* (Langebartel 1968).

Aniliidae

Anilius (Langebartel 1968), *Cylindrophis* (Lubosch 1933, Langebartel 1968).

Xenopeltidae

Xenopeltis (Langebartel 1968).

Boidae

Boa (Gibson 1966), *Calabaria* (Langebartel 1968), *Charina* (Langebartel 1968), *Constrictor* (Langebartel 1968), *Epicrates* (Langebartel 1968), *Eryx* (Langebartel 1968), *Eunictes* (Anthony and Serra 1950, Langebartel 1968), *Liasis* (Langebartel 1968), *Python* (Lubosch 1933, Edgeworth 1935, Kesteven 1944, Frazzetta 1966, Langebartel 1968, Oldham, Smith, and Miller 1970), *Sanzinia* (Langebartel 1968), *Trachyboa* (Langebartel 1968).

Colubridae

Achalinus (Langebartel 1968), *Achrochordus* (Langebartel 1968), *Amblycephalus* (Langebartel 1968), *Aparallactus* (Langebartel 1968), *Atretium* (Langebartel 1968), *Cerberus*.(Langebartel 1968), *Chersydrus* (Langebartel 1968), *Coluber* (Walter 1887), *Dasypeltis* (Langebartel 1968), *Dryophis* (Lubosch 1933), *Elaphe* (Albright and Nelson 1959, Langebartel 1968), *Enhydrus* (Langebartel 1968), *Fimbrios* (Langebartel 1968), *Haplopeltura* (Langebartel 1968), *Heterodon* (Langebartel 1968), *Mehylya* (Langebartel 1968), *Natrix* (Sondhi 1958), *Nerodia* (Langebartel 1968, Oldham, Smith, and Miller 1970, Varkey 1979), *Nothopsis* (Langebartel 1968), *Opheodrys* (Cundall 1974), *Pituophis* (Oldham, Smith, and Miller 1970), *Sibynomorphus* (Langebartel 1968), *Sibynophis* (Langebartel 1968), *Thamnophis* (Langebartel 1968, Oldham, Smith, and Miller 1970), *Tropidonotus* (Lubosch 1933), *Xenodermus* (Langebartel 1968), *Xenodon* (Langebartel 1968).

Elapidae

Denisonia (Langebartel 1968), *Doliophis* (Langebartel 1968), *Naja* (Lubosch 1933, Langebartel 1968), *Notechis* (Langebartel 1968), *Pseudechis* (Kesteven 1944).

Hydropidae

Aipysurus (Langebartel 1968), *Hydrophis* (Langebartel 1968), *Laticauda* (Langebartel 1968), *Pelamis* (Langebartel 1968).

Viperidae

Aspis (Langebartel 1968), *Atractaspis* (Langebartel 1968), *Causus* (Haas 1952, Langebartel 1968), *Cerastes* (Langebartel 1968), *Echis* (Langebartel 1968), *Vipera* (Edgeworth 1935, Langebartel 1968).

Crotalidae

Agkistrodon (Langebartel 1968, Kardong 1973), *Bothrops* (Langebartel 1968), *Crotalus* (Langebartel 1968, Oldham, Smith, and Miller 1970), *Lachesis* (Lubosch 1933, Langebartel 1968).

Crocodilia

Crocodylidae

Alligator (Reese 1915, Lubosch 1933, Edgeworth 1935, Chiasson 1962, Poglayen-Neuwall 1953b), *Caiman* (Schumacher 1973), *Crocodylus* (Camp 1923, Edgeworth 1935, Kesteven 1944, Sondhi 1958, Poglayen-Neuwall 1953b).

Gavialidae

Gavialis (Sondhi 1958).

IV. BUCCAL FLOOR MUSCLES ASSOCIATED WITH THE HYOID APPARATUS

1. M. geniohyoideum (genioglossus)

The M. geniohyoideus originates on the mandible and inserts on the hyoid apparatus. In *Lissemys* the M. geniohyoideus consists of two bundles arising from the mandible and inserting on the second ceratobranchial. Two distinct parts of this muscle arise from separate although continuous sites on the mandible in *Trionyx*. Each part inserts individually on the second ceratobranchial. According to Sondhi (1958) one of these, the portio dorsalis, arises from the ventral surface of the second ceratobranchial. The other, the portio ventralis, lies ventral to the portio dorsalis and dorsal to the Mm. mylohyoideus posterior and constrictor colli; it inserts on the second ceratobranchial just posterior to the portio dorsalis.

In *Deirochelys* and *Chelodina* one part (M. genioglossus) arises from the anterior end of the inner border of the dentary and inserts on the basihyoid. Another portion (M. geniohyoideus) arises from the inner side of the mandibular symphysis and passes posteriorly to insert on the proximal end of the hyoid cornua. A similar condition exists in *Lissemys* and *Geochelone elegans* except that the median fibers also insert on the median raphe.

The M. geniohyoideus of *Alligator* is a slender muscle separated into two bundles. The medial bundle inserts onto the second ceratobranchial, whereas the lateral attaches to the M. sternohyoideus. The M. geniohyoideus of *Gavialis* lies obliquely in the posterior part of the buccal floor, where it originates posteriorly along the inner border of the mandible; it extends posteriorly and medially to become a tendon at its insertion near the middle of the ventrolateral border of the ceratobranchial. In *Crocodylus* the M. geniohyoideus inserts on the ventrolateral aspect of the proximal part of the second ceratobranchial.

In *Sphenodon* (Byerly 1926) and *Chamaeleo* (Gnanamuthu 1937) it is narrow, whereas in *Mabuia, Cabrita, Anolis* (Gnanamuthu 1937), *Amblyrhynchus, Brachylophus, Chalarodon, Conolophus, Ctenosaura, Cyclura, Dipsosaurus, Iguana, Oplurus, Sauromalus* (Avery and Tanner 1971), *Hemidactylus, Coleonyx, Tarentola* (Figs. 4, 5), *Chlamydosaurus* (Beddard 1906), *Uromastyx, Xenosaurus* (Haas 1960), *Cnemidophorus* (Fisher and Tanner 1970, Presch 1971), *Heloderma, Gerrhonotus* (Camp 1923), *Anniella* (Bellairs 1950), *Shinisaurus* (Haas 1960), and *Dibamus* (Girgis 1961, Gasc 1968) it forms a broad sheet arising from the posteromedial border of the mandible and passing posteriorly. There it is divided into three to six slips that may interdigitate with the M. mylohoideus (Fig. 18 A, B, C, D). The superficial lateral slips overlie the medial one posteriorly and insert on the first ceratobranchial ventral to the medial muscle. A deep lateral slip originates on the mandible dorsal to the

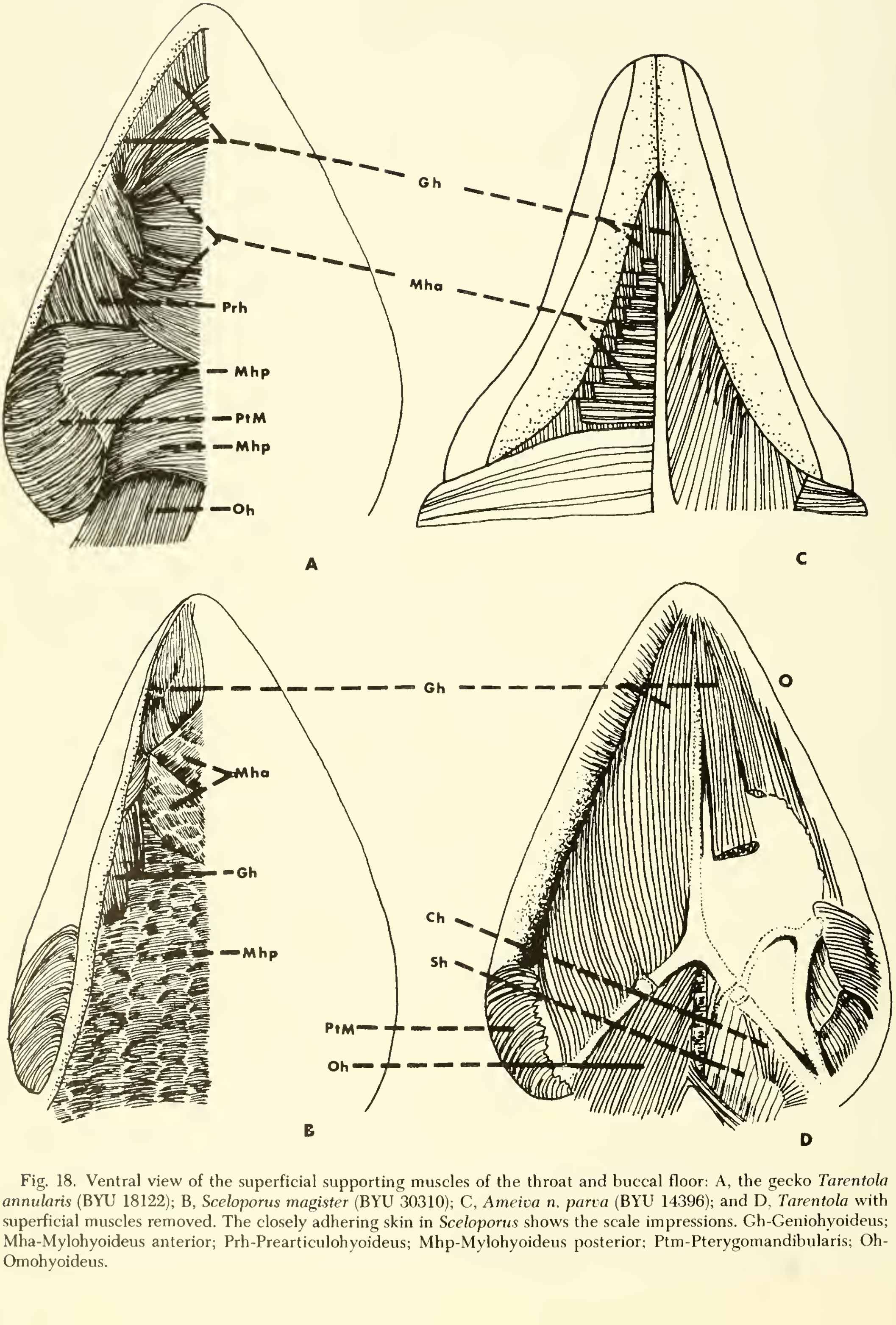


Fig. 18. Ventral view of the superficial supporting muscles of the throat and buccal floor: A, the gecko *Tarentola annularis* (BYU 18122); B, *Sceloporus magister* (BYU 30310); C, *Ameiva n. parva* (BYU 14396); and D, *Tarentola* with superficial muscles removed. The closely adhering skin in *Sceloporus* shows the scale impressions. Gh-Geniohyoideus; Mha-Mylohyoideus anterior; Prh-Prearticulohyoideus; Mhp-Mylohyoideus posterior; Ptm-Pterygomandibularis; Oh-Omohyoideus.

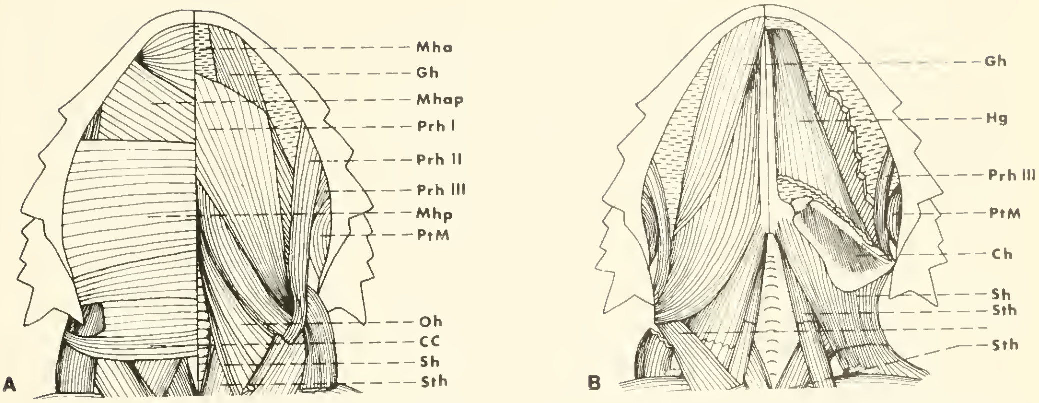


Fig. 19. Ventral view of *Phrynosoma platyrhinos*: A, Superficial myology; B, deeper muscles. (After Jenkins and Tanner 1968)

lateral superficial slip and inserts on the distal end of the epihyal.

The geniohyoideus in *Varanus* arises from the ventromedial border of the posterior part of the mandibular ramus and fans out posteriorly to cover the buccal floor and neck. The fibers converge posteriorly to insert on the ventromedial border of the proximal end of the second ceratobranchial and basihyoid, and the more median fibers insert in the fascia of the sternohyoideus and omohyoideus muscles. In the Iguanidae the medial fibers insert on the basihyoid or the anterior margin of the first ceratobranchials (Fig. 19), whereas in the gekkonids (*Tarentola* and *Coleonyx*) fibers are loosely divided into two bundles, the inner one inserting on the basihyoid and the other attached along the anterior margin of the first ceratobranchial (Fig. 18 D).

The M. geniohyoideus (genioglossus of Avery and Tanner 1971) of the iguanine lizards consists of three parts, including the anterior fibers that arise on the ventromedial border of the mandible, where its fibers interdigitate with the M. intermandibularis anterior profundus and extend posteriorly (Fig. 18). There, the more medial fibers may insert on the lingual process, with the remainder passing ventral to the anterior cornu to insert on the first ceratobranchial (Fig. 19). A second division originates on the midventral raphe and inserts on the anterior border of the first ceratobranchial, with the third portion originating on the ventromedial border of the mandible, and interdigitates (as does the first part) before inserting on the lateral border of the first ceratobranchial. A muscle deep to the lateral slip originates on the mandible and inserts on the posterior edge of the epihyal. This muscle may easily be included as a part of the lateral slip of the geniohyoideus. Jenkins and Tanner (1968), following Oelrich (1956), referred to it as the M. mandibulohyoideus III (Fig. 20). We have modified their designation to the M. mylohyoideus III, and wonder if the muscle is not a part of the M. geniohyoideus adapted to strengthen the lateral part of the mandibular-hyoid-buccal floor. We note that the same muscle is present in *Agama*, but less massive than in iguanids.

In the scincid *Eumeces* (Nash and Tanner 1970), the M. geniohyoideus originates from the anteromedial fifth of the mandible and inserts posteriorly by medial and lateral slips onto the hypoglossus, lingual fascia, and anterior margin of the first ceratobranchial. Some fibers also insert dorsally on the oral membrane and anteromedially on the cutaneous fascia.

Fisher and Tanner (1970) describe the M. geniohyoideus in *Ameiva* and *Cnemidophorus* (Teiidae) as originating on the medial surface of the dentary and inserting as five slips along the anterior margin of the body of the hyoid and the first ceratobranchial. Some dorsal fibers appear to insert on the ventral portion of the tongue. In these genera there is considerable interdigitation of the transverse and longitudinal muscles, as seen in Figure 18 C.

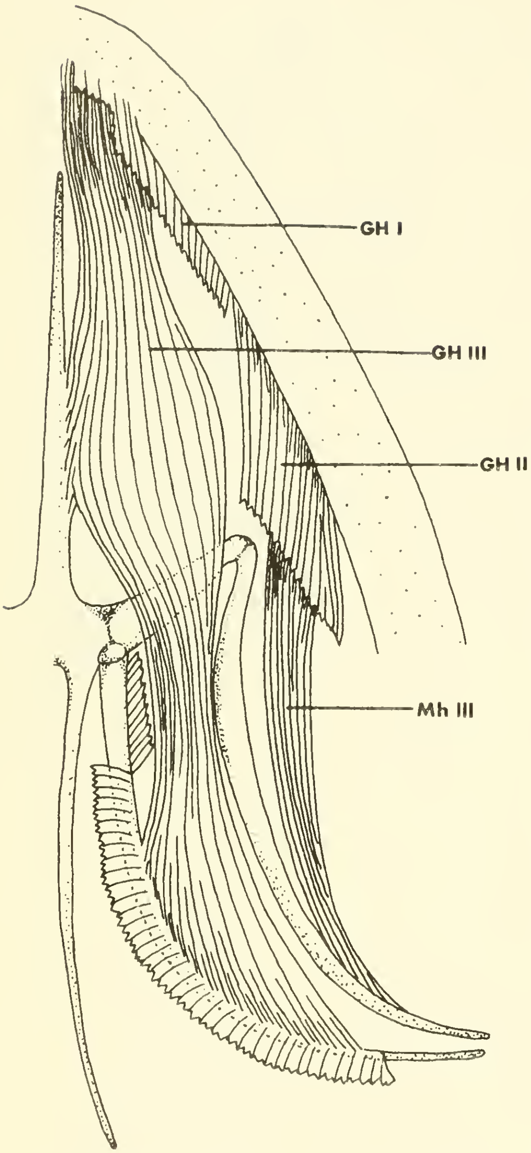


Fig. 20. Ventral view of the M. geniohyoideus of *Sauromalus* (BYU 32551) showing the origins (along mandible) and insertions (on hyoid apparatus). Gh-I-II-III divisions of the genioglossus and Mh III mandibulohyoideus.

In *Calotes, Sitana*, and *Chamaeleo* (Fig. 18) the median bundle is similar to that of the geckos, but there are two lateral bundles in *Calotes* and *Chamaeleo* and four in *Sitana*. In *Chamaeleo* the two lateral bundles are deeper and insert on the ceratobranchial. The most medial of these bundles also has an insertion on the anterior cornu. In *Draco* there are four lateral bundles, but the median bundle is missing. One of the lateral bundles interweaves with the M. mylohyoideus anterior and another (M. geniohyoideus basibranchialis of Gnanamuthu 1937) is attached to the branchial process. The lateral bundles of the M. geniohyoideus of *Chamaeleo* and *Draco* produce the M. adductor inferior labioris of Gnanamuthu (1937) (Fig. 21).

In *Agama agama* the median fibers do not insert on the basihyoid, but extend ventral to it and insert on the first ceratobranchial. The anterior cornu and body of the hyoid are covered ventrally by the M. geniohyoideus. The deep lateral slip inserts on the epihyal and, except for its smaller size, is similar to that seen in the iguanids.

In snakes such as the anomalepidids, the M. geniohyoideus arises from the posterior half of the mandible and passes posteriorly as a broad sheet separated medially from its counterpart by the linea alba. It inserts on both the basihyal and the second ceratobranchial. In the anomalepidids a slender slip of muscle attaches to the tip of the dentary and the terminal part of the second ceratobranchial; it has been described by Langebartel (1968) as being either another portion of the M. geniohyoideus or the M. ceratomandibularis. In the anomalepidids there is some variation in this muscle. The origin is by a single head in the Leptotyphlopidae and in the genera *Rhinophis, Cylindrophis rufus, Sanzinia, Enhydris, Aidpysurus*, and *Bothrops*. There is more than one head of origin in the Typhlopidae and Uropeltidae.

Another portion of this complex (M. geniohyoideus of Langebartel 1968) is described as occurring only in the Anomalepididae, in which it originates from the posterior half of the lower jaw and inserts on the hyoid cornua and ceratobranchial. In *Natrix* (*Xenochrophis*) the M. geniohyoideus is covered ventrally by the Mm. mylohyoideus posterior and constrictor colli after arising from the ventromedial border of the mandible. The parallel fibers of the M. geniohyoideus insert on the lateral border of the basihyoid and the anterior border of the second ceratobranchial after passing obliquely to the midline. Varkey (1979) describes a second origin from the midventral raphe and fascia just anterior to

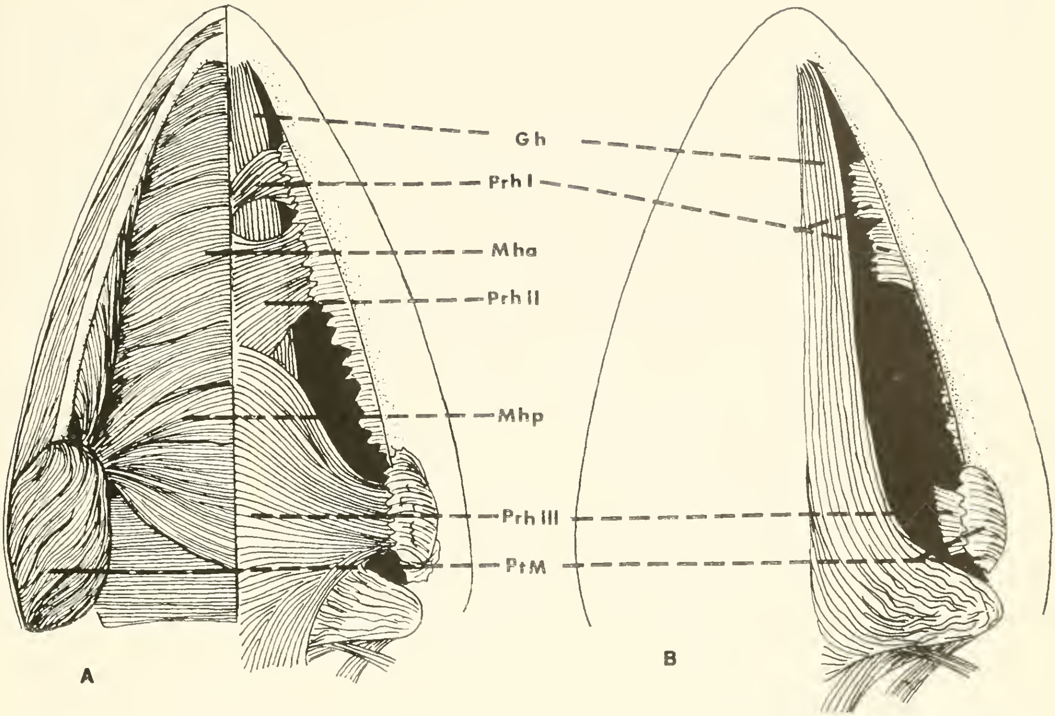


Fig. 21. Ventral view of *Chamaeleon brevicornis* (BYU 12422): A, superficial and muscles immediately dorsal to the superficial ones; B, geniohyoideus.

the lingual sheath. He considers the insertion to be the fascia of the hypoglossus muscle.

2. M. genioceratoideus

In *Varanus* the most lateral bundles of the M. geniohyoideus complex form a separate muscle (Sondhi 1958). It arises on the inner ventrolateral border of the mandible and extends posteriorly, where its fibers divide into two bundles. One bundle inserts on the lateral side of the handlelike position of the portio proximalis of the anterior cornu, with the second bundle inserting on the ventrolateral border of the middle cartilaginous part of the portio distalis of the second ceratobranchial. This muscle may exist in *Chamaeleo*, in which it has been described by Mivart (1870) as the ceratomandibular. A similar situation exists in *Chlamydosaurus* (Beddard 1950b, DeVis 1883).

3. M. prearticulohyoideus

The M. prearticulohyoideus is considered as a division of the M. genioceratoideus by Gnanamuthu (1937).

3a. M. mandibulohyoideus

In turtles, such as *Trionyx*, this muscle is large, lying in the ventrolateral region of the buccal floor and arising from the ventromedial border of the posterior part of the mandible; it inserts on the posterior region of the second ceratobranchial. In *Gavialis* the M. prearticulohyoideus is a thin muscle lying dorsal to the M. ceratohyoideus to insert on the posterior portion of the second ceratobranchial. Edgeworth (1935) has described a similar muscle in *Alligator*, which he calls the M. branchiomandibularis.

The second sheet (M. mandibulohyoideus I) is a long triangular muscle extending two-thirds the length of the mandible and lying lateral to the M. mandibulohyoideus II. This sheet originates along the ventromedial surface of the dentary and a small portion of the angular, with some fibers interdigiting with the more superficial musculature. The insertion is just posterolateral to that of the M. mandibulohyoideus II on the distal two-thirds of the posterior cornu.

The M. mandibulohyoideus, as described by Avery and Tanner (1971) for the iguanine lizards, by Robison and Tanner (1962) for *Crotaphytus,* and by Jenkins and Tanner (1968) for *Phrynosoma*, consists of two sheets. The most medial portion (M. mandibulohyoideus II) consists of a pair of small elongated bundles of fibers lying medial to the M. mandibulohyoideus I and inserting together on the midventral raphe of the throat. It originates as a narrow tendon from the mandibular symphysis. Each muscle inserts on the anterior border of the proximal end of the posterior cornu.

In *Varanus* Sondhi (1958) described it as a short muscle lying on the ventrolateral side of the neck, covering the posterior part of the mandible ventrally. It arises from the posterior and medial aspects of the mandible and extends almost straight back along the ventrolateral side of the neck to insert on the rodlike portion of the portio distalis of the anterior cornu.

4. M. mandibulopriximalis

The mandibulopriximalis has been described in *Varanus* by Sondhi (1958) as a slender muscle situated dorsal to the M. geniohyoideus and ventral to the M. genioglossus. It arises from the ventrolateral border of the ramus of the mandible, extending posteriorly and obliquely to pass dorsal to the handlelike portion of the portio distalis. Most of this muscle inserts on the outer margin of the handlelike portion of the portio proximalis, with some of its fibers becoming separated from the remainder and inserting on the lining of the buccal floor.

In the iguanid lizards the M. mandibulopriximalis, if present, forms a part of the M. geniohyoideus and cannot be distinguished from the latter muscle.

5. M. ceratohyoideus

The M. ceratohyoideus of *Sphenodon* is short and thin, having its origin on the second ceratobranchial and its insertion on the anterior cornu. Rieppel (1978) states that the presence of the M. ceratohyoideus lying between the ceratohyal and the first ceratobranchial and innervated by the M. glossopharyngeus is primitive. He further argues that its failure to reach the lower jaw, as is the case in most lizards, is also perhaps an indication of its primitiveness.

In *Lissemys* the M. ceratohyoideus arises from the second ceratobranchial and inserts on the basihyoid. In *Trionyx* it arises from the distal half of the second ceratobranchial, enclosing this cartilaginous rod and extending anteromedially on the lateral side of the buccal floor to insert on the middle and anterior components of the basihyoid and on the knoblike anterior cornu.

In *Alligator* and *Crocodylus* it originates on the second ceratobranchial and inserts on the basihyoid. In *Gavialis* the M. ceratohyoideus lies dorsal to the basihyoid and is not visible in ventral view. The origin is on the dorsolateral border of the posterior cornu, with the muscle extending obliquely forward as a thin sheet on the ventral side of the buccal floor to insert on the dorsolateral side of the anterior cornu.

The insertion in *Sitana* is on the basihyoid. In *Varanus* it lies dorsal to the M. geniohyoideus on the ventrolateral side of the middle of the neck. The origin is from the ventrolateral border of the proximal piece of the second ceratobranchial, from which the muscle extends anteromedially to fan out over the ventrolateral side of the neck and insert on the handlelike portion of the portio distalis.

In the iguanid lizards this muscle has been described as the M. branchiohyoideus by Avery and Tanner (1971). In *Ctenosaura* the muscle is ribbonlike and situated between the first ceratobranchial and second ceratobranchial of each side of the hyoid apparatus. The origin is along most of the anterior two-thirds of the first ceratobranchial, with the insertion on the posterior half of the second ceratobranchial. This pattern is duplicated in *Chalarodon*, *Oplurus*, *Crotaphytus*, and all the remaining iguanine lizards except *Sauromalus*. In the latter the insertion is very narrow, by a single tendon from the proximal rim of the anterior border of the posterior cornu.

In *Phrynosoma* this muscle covers nearly the entire area between the anterior and posterior cornua of the hyoid (Fig. 19 B). Its origin and insertion are similar to that described above for other iguanids. In *Chamaeleo* the M. ceratohyoideus is a small thick mass arising from the posterolateral border of the basihyoid to pass anterodorsally and insert on the epihyal.

In *Eumeces* (Scincidae) the muscle is a narrow strap similar to that in the iguanid *Sauromalus*.

In the teiids, *Cnemidophorus* and *Ameiva*, this muscle has a similar origin to that of the iguanids, but fills the entire area between the anterior and posterior cornua (Fisher and Tanner 1970).

6. M. cornuhyoideus

The M. cornuhyoideus was described in *Varanus* by Sondhi (1958) as being immediately posterior to the M. ceratohyoideus; it is ventrally concealed by the basal branch of the tongue and extends between the anterior and posterior cornua. It arises from the ventrolateral border of the proximal piece of the second ceratobranchial and proceeds forward to insert on the outer margin of the portio proximalis of the anterior cornu, anterior to the latter's articulation with the basihyoid. This muscle has not been described in any other reptile.

7. M. interportialis

Sondhi (1958) has reported that in *Varanus* this slender muscle lies dorsal to the M. ceratohyoideus and ventral to the portio proximalis. The origin is on the ventrolateral side of the anterior portion of the portio proximalis, from which the muscle extends obliquely anteriorly to insert on the medial border of the handlelike portion of the portio distalis. Gnanamuthu (1937) did not describe this muscle for *Varanus* and probably considered it to be part of the M. ceratohyoideus. It has not been described in other reptiles.

8. M. hypoglossolateralis

The M. hypoglossolateralis has been described by Sondhi (1958) as a delicate strip of muscle lying above the hypoglossum of the turtle *Trionyx*. Its origin is on the dorsal surface of that cartilaginous plate from which it extends to the lining of the buccal floor on which it inserts. This muscle is also present in *Gopherus agassizi*, and we suspect its presence in association with the hypoglossal cartilage of other Chelonia.

9. M. entoglossohypoglossalis

The M. entoglossohypoglassalis is another muscle described by Sondhi (1958) for *Trionyx*. It arises from the ventrolateral border of the anterior part of the lingual process and inserts dorsolaterally on the posterior surface of the hypoglossum.

10. M. omohyoideus

In turtles such as *Lissemys* the M. omohyoideus is thick and long, and has an anterior division into dorsal and ventral bundles. The dorsal bundle inserts on the medioproximal part of the first ceratobranchial, and the ventral bundle inserts on the basihyoid along with the M. sternohyoideus. In *Trionyx* the M. omohyoideus originates on the anterior border of the scapula and extends forward on the ventral side of the neck to converge anteriorly to form two bundles, a larger medial and small lateral, which insert on the proximal part of the second ceratobranchial. In *Chelodina* the M. omohyoideus arises from the middle of the coracoid, but in *Deirochelys*, *Lissemys*, and *Geochelone* it originates on the ventral end of the coracoid. In all genera the fibers pass anteriorly to insert on the ceratobranchials.

In *Alligator* the M. omohyoideus is a long, narrow, thick muscle that originates from the upper border of the coracoid and passes forward to insert on the middle of the second ceratobranchial. In *Crocodylus* the origin is from the anterior border of the scapula and the insertion on the second ceratobranchial. *Gavialis*, as described by Sondhi (1958), has a moderately broad muscle arising from the anterior border of the coracoid. As it passes anteriorly, it divides into two parts, a portio dorsalis and a portio ventralis. The portio dorsalis extends obliquely anteromedially as a narrow strap that terminates in fragile slips that merge into the tendon of the M. sternohyoideus. The portio ventralis is broad, and its fibers parallel the trachea, finally inserting on the short anterior part of the second ceratobranchial.

The M. omohyoideus is a large muscle that usually arises on the pectoral girdle and inserts on the hyoid. In *Sphenodon* it is a large sheet, but in *Varanus* it is slender and partly covered by the M. sternohyoideus along its medial border. We summarize from Gnanamuthu (1937:24) as follows: In *Varanus* it arises on the anterior border of the scapula to pass obliquely forward and insert on the anterior part of the proximal end of the second ceratobranchial close to its articulation with the basihyoid. A similar situation exists in *Hemidactylus*. In *Cabrita*, *Mabuia*, and *Chamaeleo* the insertion of the M. omohyoideus is on the anterior border of the basihyoid. In *Calotes* it inserts not only on the basihyoid, but also on the sides of the proximal part of the first ceratobranchial. In *Anolis* and *Sitana* it inserts only on the first ceratobranchial, but in *Draco* there are three bundles, two of which insert on the first ceratobranchial and the third on the second ceratobranchial. In *Chlamydorsaurus* it originates on the clavicle and sternum and inserts on the posterior one-third of the ceratobranchial.

In the iguanid lizards, such as *Ctenosaura*, the M. omohyoideus has medial and lateral origins. Medially the fibers originate on the lateral tip of the transverse process of the interclavicle, whereas the lateral fibers originate on the lateral half of the anterolateral surface of the clavicle and the anterior border of the suprascapula. As the two bundles extend anteriorly they become continuous and insert together along the posterior edge of the second ceratobranchial. In all the iguanine lizards and *Oplurus* the fibers of the medial and lateral bundles are impossible to separate. *Chalarodon* shows a slightly different configuration, with both bundles being separated for their entire length.

The M. omohyoideus in the teiids *Ameiva* and *Cnemidophorus* is a thick muscle originating on the anterior border of the scapula and then proceeding anteroventrally to insert on the proximal end of the basihyoid and along the second ceratobranchial. In *Dibamus* it is extremely long, originating on the scapula and inserting on the distal two-thirds of the ceratobranchial.

In snakes this muscle is very small and passes anteriorly from its origin on the lateral body muscles just posterior to the distal end of the hyoid apparatus to insert on the posterior portion of the ceratobranchials. It has been found in the Anomalepididae *Cylindrophis*, *Rhinophis*, and *Eryx c. colubrinus*.

11. M. sternohyoideus

The M. sternohyoideus is a complex of muscles that arises from the sternum and inserts on the hyoid in most reptiles (Fig. 19).

In both *Lissemys* and *Trionyx* the M. sternohyoideus is large and lies adjacent to the M. omohyoideus. It originates from the clavicle and passes anteriorly and medially to insert on the proximal part of the second ceratobranchial and the middle of the basihyoid. In *Crocodylus* the M. sternohyoideus has long tendons by which it inserts on the second ceratobranchials. In *Alligator* it is flat and broad, and originates from the ventral surface of the episternum and forms a short tendon that inserts on the M. geniohyoideus. In *Gavialis* the M. sternohyoideus is a broad flat muscle with an origin on the ventral anterior half of the episternum; it passes along the ventral side of the neck to meet its opposite member at the midline where it obscures the trachea ventrally (Sondhi 1958). As it approaches the hyoid apparatus it divides into two parts, with the outer part (portio externa) a broad band forming a large tendon that inserts on the inner border of the mandible. The inner bundle (portio interna) parallels the trachea to insert on the outer part of the posterior border of the basihyoid.

In *Sphenodon* it is flat, whereas in some lizards it becomes cordlike and inserts (Rieppel 1978) on the caudodorsal edge and dorsal surface of the first ceratobranchial, deep to and lateral to the insertion of the omohyoideus. In *Mabuia*, the M. sternohyoideus inserts on the basihyoid, whereas in *Anolis*, with its small basihyoid, the insertion is on the first ceratobranchial. In *Varanus* the M. sternohyoideus lies dorsal to the M. constrictor colli and ventral to the basihyoid and the proximal piece of the second ceratobranchial. It arises from the ventrolateral border of the clavicle and extends obliquely anteriorly to the ventral side of the neck, where it parallels the M. omohyoideus and inserts on the ventral side of the basihyoid and posterior portion of the lingual process. *Chamaeleo* has a small lateral bundle of fibers that insert on the fascia of the lateral M. geniohyoideus.

The M. sternohyoideus of the iguanine lizards (Avery and Tanner 1971), is an extensive muscle sheet occupying a large area posterior to the anterior cornu and anterior to the sternum and clavicle. It originates from several heads on the clavicle, and its oblique fibers extend anteriorly to insert on the posterior surface of the anterior cornu. In all the iguanines and in *Chalarodon* the muscle appears broad and sheetlike. In *Oplurus,* it is narrow and cordlike.

In *Phrynosoma* the M. sternohyoideus is separated into three distinct muscles (Fig. 19). As described by Jenkins and Tanner (1968), the M. sternohyoideus I originates from the medial surface of the scapula and the most anterior part of the clavicle and inserts on the distal two-thirds of the anterior cornu. This muscle may be the M. sternothyroideus of other workers. The M. sternohyoideus II originates from the anterolateral surface of the sternum and inserts onto the posterodorsal surface of the basihyoid.

The M. sternohyoideus III is separate for its entire length, with an origin from the ventral surface of the anterior third of the sternum and an insertion on the dorsal surface of the most enlarged area of the posterior cornu.

In the agamid *Chlamydorsaurus,* the M. sternohyoideus has a large origin from the sternum immediately deep to that of the M. omohyoideus. It expands and thins as it extends anteriorly to insert on the inner side of the ceratobranchial ventral to the M. omohyoideus. In *Uromastyx* the origin is from both the sternum and the coracoid.

Nash and Tanner (1970) describe a superficial and a deep layer of this muscle in the skink *Eumeces.* The larger ventral or superficial layer originates from the posterior and ventral surfaces of the ceratobranchial I and medial to the corpus and inserts on the interclavicle with the M. sternocleidomastoideus, trapezius, and depressor mandibularis, and with the constrictor colli on the posterior and ventral surfaces of the anterior cornu. The dorsal or deep layer originates on the interclavicle and inserts on the posterior border of both anterior and posterior cornua.

In *Dibamus,* the M. sternohyoideus is a large strap originating from the sternum and coracoid and inserting on the distal tip of the ceratobranchial (Gasc 1968).

In the teiids *Ameiva* and *Cnemidophorus,* the M. sternohyoideus is broad, with an origin on the sternum and insertions on both the posterior and anterior cornua and the basihyoid.

In snakes the M. sternohyoideus is found as a separate muscle only in the Typhlopidae and Leptotyphlopidae. Its origin here is deep to the muscles on the linea alba. The fibers pass anteriorly to insert on the hyoid, usually on the entire posterior edge of each cornu.

12. M. sternothyroideus

In the turtle *Trionyx* the origin of the M. sternothyroideus is on the anterior border of the sternum. The muscles extend anteriorly to insert on the ventrolateral border of the posterior part of the basihyoid.

In lizards, the M. sternothyroideus normally has an origin on the anteromedial portion of the sternum, from which it extends anteriorly to insert along the length of the second ceratobranchials. This situation exists in *Hemidactylus, Mabuia, Cabrita, Anolis, Calotes,* and the iguanine lizards. In *Chamaeleo* the M. sternothyroideus extends laterally to insert on the distal end of the ceratobranchial. In *Varanus* the M. sternothyroideus lies dorsal to the Mm. omohyoideus and sternohyoideus. It originates as a thin sheet from the anteromedial half of the sternum and inserts on the anterior half of the proximal piece of the second ceratobranchial.

In the iguanine lizards the most medial series of fibers of the M. sternohyoideus complex, the M. sternothyroideus, may be separated from the other members of this group by their different origins and insertions. The origin consists of a small area of both the interclavicle and sternum. These fibers pass anteriorly and parallel to the trachea to insert on the basihyoid. Along its length this muscle is difficult to separate from the more lateral M. sternohyoideus, except in *Oplurus* and *Chalarodon,* in which both muscles are free and separated along their entire length.

The M. sternothyroideus of *Phrynosoma* was previously described by Jenkins and Tanner (1968) as the M. sternohyoideus I.

13. M. costocutaneous superior

Because the shoulder girdle of snakes has been lost, the M. omohyoideus, sternohyoideus, and sternothyroideus cannot be identified. Therefore these muscles will be discussed here under the name M. costocutaneous superior.

In some snakes it is possible tentatively to identify the homologs of these three muscles. For example, in the Typhlopidae and the Leptotyphlopidae, the M. sternohyoideus is a distinct mass of fibers that arise from the ventral scales and adjacent rows of lateral scales and the ribs, extending anteriorly to the hyoid and surrounding muscles. In *Typhlops, Leptotyphlops, Rhinophis, Cylindrophis,* and *Achrochordus,* the anteriormost fibers of the complex extend to originate on the mandible and overlay the hyoid while having no connection with it. In *Cylindrophis* the fibers originate on the posterior or medial edge of the M. constrictor colli. In the anomalepidid snakes the insertion is on the posteromedial border of the basihyoid and second ceratobranchial. The insertion also extends to the base of the lingual process in most specimens. In *Agkistrodon, Bothrops,* and *Crotalus,* the insertion is most extensive on the median raphe and lingual process.

Sondhi (1958) describes three specific muscles present in *Natrix* (*Xenochrophis*) that are probably homologous to the Mm. omohyoideus, sternohyoideus, and sternothyroideus. The omohyoid portion arises from the skin on the ventrolateral part of the neck and then extends obliquely anteriorly to insert on the ventrolateral aspect of the basihyoid. In *Atretium,* this muscle has a cutaneous origin and inserts on the second ceratobranchial. The second muscle, absent in *Atretium* but possibly the M. sternohyoideus, originates from the skin in the ventrolateral region of the neck posterior to the M. omohyoideus and passes anteriorly to close proximity with the latter to insert on the outer border of the basihyoid. The sternothyroid part of this complex lies in the midline of the neck over the ventral surface of the basihyoid, with its origin on the midventral portion of the cervical skin. The muscle inserts on the medial border of the basihyoid. In *Atretium* the sternothyroid portion of the complex has its origin from the second ceratobranchial, with some fibers intertwining with their opposite member at the midline.

14. M. neurocostomandibularis

According to Langebartel (1968), the M. neurocostomandibularis is present in all snakes except the Anomalepididae. In most snakes it is a broad sheet forming part of the M. neurocostomandibularis complex, but in some it is separate and narrow. It covers a large area of the head and in some is partially overlain by the Mm. constrictor colli and costocutaneus superior. Its origin is on the dentary, from which it proceeds posteriorly to insert variously on the hyoid apparatus.

The muscles of *Python sebae* (Frazzetta 1966) and *Boa constrictor* (Gibson 1966) that are innervated by the hypoglossal nerves form a single muscular complex, the M. neurocostomandibularis, and correspond roughly to the M. geniohyoideus of other reptiles. The complex extends between the mandibles and the second ceratobranchials. In both *Boa* and *Python* the origin is on the lower jaw and the insertion on the posterior part of the second ceratobranchial.

In *Natrix* (*Xenochrophis*), Sondhi (1958) describes the M. neurocostomandibularis as probably the M. geniolateralis because the latter muscle receives a branch from the hypoglossal nerve. Langebartel (1968) considered this muscle to be the M. ceratomandibularis as designated by Richter (1933). The proper identity of this muscle in the typhlopids, leptotyphloids, and anomalepidids is unknown to us. According to Langebartel (1968), the M. ceratomandibularis in snakes arises from the dentary and inserts on the anterior part of the hyoid and the tendinous inscription in the M. neurocostomandibularis.

Varkey (1979) describes the M. neurocostomandibularis as being very complex and having three separate heads in *Nerodia.* It is a wide flat muscle sheathing the neck and most of the lower jaw. One origin (the vertebral head) is on the apponeurosis of the dorsal midline neck region. It passes under the constrictor colli to insert on the midline raphe. The costal head originates by narrow slips from the first seven anterior ribs and inserts on the midline raphe with the previous slips. The third or hyoid head has a double origin from the midventral raphe just median to the hyoid cornua. This branch is called M. transversalis branchialis by Langebartel (1968). It inserts on the origin of the other heads on the midline raphe.

15. M. transversalis branchialis

The M. transversalis branchialis appears variably and erratically in the families of snakes with the exception of the Anomalepididae, Typhlopidae, and Leptotyphlopidae, in which it is universally absent.

When present, this muscle arises from somewhere on the second ceratobranchial. In *Rhinophis*, the origin is on the medial edge, whereas in *Cylindrophis* it originates on the anterior two-thirds. In *Anilius* the entire length of the cartilage is involved.

The insertion of this muscle is usually on the median raphe, although in some snakes it is inserted on the fascia covering the M. costocutaneous superior.

In *Nerodia*, Varkey (1979) describes the M. transversus branchialis as originating on the midline raphe just anterior to M. intermandibularis's anterior. It passes anterolaterally to insert broadly on the mucosa of the angulo-splenial articulation and narrowly on the lateral sublingual gland. Varkey indicates his usage of this muscle name is as in Albright and Nelson (1959), Cowan and Hick (1951), and Weaver (1965). Langebartel (1968) calls this muscle the dilator of the sublingual gland, using the name M. transversalis branchialis for a branch of what Varkey calls the M. neurocostomandibularis.

16. M. hyotrachealis

In most snakes the M. hyotrachealis arises from the second ceratobranchial, but in *Liotyphiops* and the leptotyphiopids the fibers are tied by connective tissue on the ventrolateral surface of the lining of the buccal floor. In the typhlopids the fibers originate in connective tissue on the hypaxial trunk muscles. In other snakes the M. hyotrachealis originates on the lateral edge of the second ceratobranchial. In *Rhinophis* the origin is at the anterior quarter of the medial edge, while in *Cylindrophis maculatus* and *C. rufus* the origin is from the lateral edge about halfway down the ceratobranchial. In the boids it originates on the posterior half of the cartilage. In *Tropidophis* the origin is deep from the raphe of the M. neurocostomandibularis. In colubrids, viperids, and elaphids the origin varies extensively. In *Heterodon* and *Pseudaspis* the origin varies extensively. In *Heterodon* and *Pseudaspis* the origin is from the rib cage, while in *Agkistrodon* it may be either the rib cage or hyoid, indicating a split origin. In *Vipera aspis*, Edgeworth (1935) describes one head of the M. hyotrachealis as lying dorsal to the rib cage while the lateral head attaches to the hyoid. In *Cerastes* the single head originates from the ventral lining of the buccal floor.

The insertion of the M. hypotrachealis is normally from the trachea of the laryngeal-tracheal area, dorsal and anterior to the insertion of the M. geniotrachealis. In some genera (*Typhlops*, *Amblycephalus*, *Xenopeltis*, and *Agkistrodon piscivorus*) the insertion is on the ventral portion of the M. geniolateralis. In *Boa cookii*, *Notechis*, and others the M. hypotrachealis has a split insertion with attachments on dorsal and ventral sides of the geniotrachealis.

Varkey (1979) describes *Nerodia*'s hyotrachealis as thin and narrow and of a double origin. One head is just anterior to a transverse tendinous inscription of the M. neurocostomandibularis. The second or median head is from the lateral edge of the hyoid cornua. The heads join and insert on the larynx and trachea anterior to the insertion of the geniotrachealis.

V. Buccal Floor Muscles Not Associated with the Hyoid Apparatus

The homologies of a number of the reptilian throat muscles not connected with the hyoid are unclear. We will present the most widely used terminology and present synonyms only when two or more names have had wide usage for the same muscle. Although the following muscles are not directly attached to the hyoid apparatus, they have a close functional relationship and are therefore included (Figs. 18, 19, 20).

1. M. constrictor superficialis

The M. constrictor superficialis is found in *Trionyx* as a superficial muscular sheet lying ventral to the anterior region of the neck. It arises as a narrow slip from the skin covering the side of the neck and broadens to insert on the gular septum. In *Gavialis* it originates on the skin overlaying the angle of the jaw, surrounds the neck, and extends obliquely to insert on the gular septum.

In other reptiles, such as iguanid lizards, this muscle is probably homologous to much of the Mm. constrictor colli and intermandibularis posterior of Avery and Tanner (1971).

2. M. constrictor colli

The M. constrictor colli is an extensive superficial muscular sheet, originating on the middorsal aponeurosis of the neck and extending ventrad to insert on the posterior part of the midventral raphe or gular septum. In *Sphenodon* it forms a broad, thin, superficial sheet that completely encases the neck (Rieppel 1978, Fig. 1). It ensheathes the entire neck in *Chelodina* and *Deirochelys*, but in *Lissemys* the neck is only partly covered. The muscle arises from the dorsal fascia and inserts on the median raphe. It is continuous anteriorly with the M. intermandibularis. Sondhi (1958) lists this muscle as present in *Trionyx* and *Gavialis*, and Gnanamuthu (1937) recognized it in *Crocodylus* and *Trionyx*. In the Testudines and Crocodylia the M. constrictor colli is not attached to the hyoid, but has an insertion on the gular septum.

This muscle covers most of the lateral surface of the neck in *Amblyrhynchus*, *Chalarodon*, *Cyclura*, *Iguana*, and *Sauromalus*. It is much less extensive in *Brachylophus*, *Conolophus*, *Ctenosaura*, *Dipsosaurus*, *Oplurus*, *Crotaphytus*, and *Phrynosoma*.

In *Chamaeleo* the M. mylohyoideus posterior of Mivart (1870) corresponds to the M. constrictor colli. It originates on the occipital crest and inserts on the median raphe.

In the skink *Eumeces* the M. constrictor colli is a very broad sheet originating from the middorsal tympanic fascial and inserting on the median raphe. It covers most of the neck from the angle of the jaw to the interclavicle.

In the teiids *Cnemidophorus* and *Ameiva*, the muscle is as in *Eumeces*, but the anterior border interdigitates with the posterior border of the M. cervicomandibularis. Gnanamuthu (1937) figures this muscle to be in *Hemidactylus*, *Mabuia*, *Cabrita*, *Anolis*, *Calotes*, and *Draco*.

In snakes the M. constrictor colli appears erratically and is not constant in form within a single genus as indicated by *Python*. The muscle is normally broad and envelops the angle of the jaw with an insertion on the midventral raphe or hyoid. In some species of *Python* it appears to be absent. The M. constrictor colli is found in all families of snakes except in the Uropeltidae where it has not been recognized.

3. M. mylohyoideus anterior

The superficial M. mylohyoideus anterior is generally located ventrally beneath the rami of the lower jaw anterior to the M. constrictor colli. It takes its origin from the anterior part of the mandible and inserts on the gular septum.

In *Sphenodon* the M. mylohyoideus (M. intermandibularis of Rieppel 1978) forms a single large muscular sheet, but in lizards it is differentiated into three sets; the Mm. mylohyoideus anterior superficialis (= M. intermandibularis anterior superficialis), mylohyoideus anterior principalis (= M. intermandibularis anterior profundus), and mylohyoideus anterior profundus (= M. intermandibularis posterior). In some forms, such as *Cabrita*, *Anolis*, *Hemidactylus*, and *Mabuia*, some fibers of the M. mylohyoideus anterior originate deep on the medial surface of the mandible and others originate superficially on the M. geniohyoideus. As the fibers of the two muscles cross, they break into numerous strips and interdigitate (Figs. 18, 19, and 20).

In turtles the M. mylohyoideus is simpler. In *Trionyx* it consists of a single M. mylohyoideus anterior profundus that originates ventral to the M. geniohyoideus from the ventral aspect of the mandible and passes medially to insert on the gular septum. In *Lissemys* the M. mylohyoideus anterior forms as two muscles, with the M. mylohyoideus anterior profundus being identical to that of *Trionyx*. The M. mylohyoideus anterior principalis is a broad sheet originating on the mandible and inserting on the gular septum.

In *Chelodina* and *Deirochelys* the intermandibular series is simple and undivided, originating on the inner surface of the mandible and inserting on the median raphe. In *Chelodina* the anterior quarter of the fibers do not insert into each other as in *Deirochelys*, but are separated by fascia.

Some age variation in this muscle can be seen in *Crocodylus*: in adults the M. mylohyoideus anterior is not distinguishable as a separate muscle, but there are two sheets in the juvenile representing the M. mylohyoideus anterior and mylohyoideus posterior. In adult *Alligator* a single transverse sheet is present (Mm. intermaxillaris and sphincter colli), and in *Gavialis* the one sheet (M. mylohyoideus anterior principalis) is probably homologous to both the Mm. mylohyoideus anterior and mylohyoideus posteri or. In *Gavialis* this muscular sheet occupies almost the entire anterior part of the ventral inter-ramal area of the neck, originating on the inner side of the mandible and inserting on the gular septum.

The M. mylohyoideus anterior superficialis exhibits several variations. In *Mabuia* and *Anolis* the fibers extend anteriorly, overlapping the M. mylohyoideus anterior principalis either medially or laterally. In the Chamaeleonidae and Agamidae the Mm. mylohyoideus anterior principalis and mylohyoideus anterior profundus occur together in the form of a double sheet, which we have concluded is a variation of the M. mylohyoideus anterior. In *Varanus*, Sondhi (1958) indicates that the muscle extends transversely from the mental groove to the M. genioglossus portio major. There are three sets of fibers listed, including a broad M. mentalis superficialis, that originate ventrally, whereas the narrow M. mentalis profundus anterior and the M. mentalis profundus posterior orig inate dorsally. All three bundles insert in the lining of the buccal floor. These muscles do not appear to be homologous to the muscular complex we have seen in iguanids and designated the M. mylohyoideus anterior.

In *Amblyrhynchus*, *Brachylophus*, *Chalarodon*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, *Oplurus*, and *Sauromalus* two distinct groups of muscle fibers are found. The M. intermandibularis anterior are deep fibers that originate as a tendon from the coronoid and splenial bones and extend medially on the ventral surface to join at the median raphe, where they interdigitate with about five bundles of the M. geniohyoideus. A small bundle of fibers also extends from the origin to insert on the connective tissue capsule of the sublingual gland. In *Iguana* this muscle forms the bulk of the large dewlap.

The most superficial group of fibers (M. intermandibularis anterior superficialis) is small and narrow, with an origin from the oral membrane and from the anterior part of the M. intermandibularis anterior profundus. The muscle fibers pass obliquely posteriorly to insert on the median raphe. In *Iguana* and *Dipsosaurus* this superficial group is greatly reduced in size.

In snakes the synonymy of the throat musculature is not well established. For this reason we follow rather closely the studies of Langebartel (1968) and Sondhi (1958). The anteriormost set of transverse fibers (M. intermandibularis anterior) is absent in *Anilius* and *Xenopeltis*, but is represented by a tendon in *Rhinophis*. In the anomalepidids, typhlopids, and leptotyphlopids this muscle is broad and may actually represent several muscles. In the latter families one or more muscle groups may originate on the medial surface of the dentary. In the colubrids, viperids, and elapids a single muscle is large but separated into two parts. The longer and thicker anterior one originates on the medial surface of the tip of the dentary and medially to the fibrous inter-ramal pad. The second (posterior) part extends obliquely from the same origin to insert on the ventral raphe. The M. mylohyoideus anterior in *Natrix* (*Xenochrophis*) is probably represented by three muscles: Mm. intermaxillaris, mentalis profundus anterior, and mentalis profundus posterior. The M. intermaxillaris originates from the ventrolateral border of the dentary and passes obliquely posteriorly to insert on the mental groove. The remaining pair of bundles originate from the mental groove and extend obliquely caudad to insert adjacent to each other on the lining of the buccal floor.

The intermandibularis anterior of *Nerodia* is described as having two separate parts. The M. intermandibularis anterior pars mucosalis has two portions. The first is a small triangular anterior portion that originates on the midventral raphe of the lower jaw and buccal membrane fascia. It inserts on the ventromedial surface of the anterior tip of the dentary and the ligament attached to it. The much stouter posterior slip originates from the midventral raphe of the lower jaw and fascia surrounding the tongue sheath just posterior to the insertion of the anterior slip. The fibers pass anterolaterally to insert on the ventromedial surface of the dentary immediately posterior to the insertion of the anterior slip.

The second part (M. intermandibularis anterior pars glandularis) originates on the midventral raphe of the lower jaw of the fibrous inter-ramal pad. The fibers pass posterolaterally to insert on the ventrolateral side of the sublingual gland at its posterior end. A small number of fibers insert on oral mucosa posterior to the gland.

4. M. mylohyoideus posterior

The M. mylohyoideus posterior is a transverse muscle situated posterior to the M. mylohyoideus anterior.

The M. mylohyoideus posterior [M. mylohyoideus anterior principalis of Sondhi (1958)] of *Trionyx* and *Lissemys* originates from the border of the mandible, where it forms a broad, thick sheet muscle. It extends medially to insert on the gular septum.

In *Alligator, Crocodylus,* and *Gavialis* the M. mylohyoideus posterior is represented by a thin sheet that combines into one muscle, the M. mylohyoideus anterior and M. mylohyoideus posterior.

In some lizards (*Mabuia* and *Cabrita*) these muscular sheets are continuous, but show a small division between them. Sondhi (1958) reports that in *Varanus* they are differentiated into two muscles (Mm. mylohyoideus anterior superficialis and mylohyoideus anterior principalis) that are disposed one behind the other, both originating on the lateral surface of the mandible and inserting on the gular septum.

In the iguanine lizards, an anterior and a posterior sheet of muscle fibers (M. intermandibularis posterior) form the M. mylohyoideus posterior. The anterior sheet is broad and thin, with an origin from the lateral surface of the mandible. The fibers pass medially on each side to insert with their opposite members at the median raphe. The posterior bundle of fibers (about one-quarter of the posteriormost fibers) originate from the lateral surface of the mandible beginning at the midpoint of the retroarticular process and insert on the linea alba.

In most iguanines the M. mylohyoideus posterior exhibits a primitive condition by being continuous with the M. constrictor colli, from which it can be delineated by a natural separation along the entire border only in *Conolophus* and *Ctenosaura.* In *Cyclura* and *Sauromalus* this separation is present only in the medial third of their common border. In *Amblyrhynchus, Brachylophus, Chalarodon, Dipsosaurus, Iguana,* and *Oplurus* the two muscles are continuous along their entire border.

In *Crotaphytus* the Mm. mylohyoidei anterior and posterior form one continuous sheet with no separation between them. In *Phrynosoma* the M. mylohyoideus posterior is separated from the anterior, but is continuous posteriorly with the M. constrictor colli, from which it can be separated only with great care.

In *Eumeces* the position of M. mylohyoideus posterior is similar to that of the iguanid lizards, with both anterior and posterior muscles being separated.

In the teiid *Ameiva* the M. mylohyoideus posterior originates on the medial surface of the dentary and immediately breaks into nine separate divisions that interdigitate with slips of the M. geniohyoideus. It inserts on the midventral raphe just posterior to the M. mylohyoideus anterior (Fig. 17). In *Cnemidophorus* the muscle is as above, except that there are only five divisions instead of the nine in *Ameiva.* The Mm. mylohyoideus posterior and constrictor colli are continuous for their entire border in *Shinisaurus,* but widely separated in *Xenosaurus.*

All snakes except one colubrid (*Amblycephalus kuangtunensis*) possess a M. mylohyoideus posterior (Langebartel 1968). It lies in the same position as the M. intermandibularis posterior of Langebartel (1968), with the former having its origins on the mandible and insertion on the gular septum. In the colubrid *Achrochordus* it is very broad, attaching to the middle region of the mandible. In *Haplopeltura boa* it is attached lateral to the external adductor muscle of the lower jaw. The fibers are not attached to the mandible, but cross their opposite members at the midventral raphe and interdigitate, eventually attaching to the opposite mandible. M. mylohyoideus inserts on the lingual process in the hydrophid *Aipysurus*.

The second bundle of fibers (M. intermandibularis posterior superficialis) is small and restricted in some snakes with the parallel type of hyoids. Its occurence is sporadic in colubrids, and it is absent in most poisonous snakes, including the hydrophids. It may be replaced by a tendon that originates from the posterior part of the lower jaw and inserts on the gular septum. Sondhi (1958) states that the M. mylohyoideus posterior is an extremely broad muscle sheet, lying immediately posterior to the M. mylohyoideus anterior and occupying the posterior region of the neck in *Natrix piscator.* He further states that this muscle originates on the dorsolateral surface of the anterior cervical vertebrae and extends ventrally to insert on the posterior part of the gular septum. Langebartel (1968) describes two muscles, a ventral sheet taking its origin from the anterior part of the mandible and extending obliquely anteriorly over the body of the tongue to insert on the gular septum, and a dorsal sheet deep and dorsal to the M. geniohyoideus, with an origin from the mandible with the ventral sheet; the dorsal sheet extends obliquely anteriorly also to insert on the gular septum. The M. ceratomandibularis of Langebartel (1968) occurs in most snakes, although with considerable variation. Because of its location, we include it as a synonym of M. mylohyoideus posterior, even though we are aware that most homologies must yet be proven by careful embryonic study.

The intermandibularis posterior of *Nerodia* is described by Varkey (1979) as having two slips. The M. intermandibularis posterior pars anterior is the largest of the ventral constrictors originating on the midventral raphe of the lower jaw ventral to the origin of the posterior slip of the intermandibular anterior I and the transversalis branchialis. The origin is broad and thin, passing caudolaterally to form a stout band to insert on the ventromedial surface of the bone at the distal end of the mandibular fossa.

The second slip, which Varkey calls the M. intermandibularis posterior pars posterior, is a thin, flat, triangular sheet of muscle that originates on the midventral raphe posterior to the origin of the intermandibularis posterior I and the transversalis branchialis and the anterior tip of the hyoid cornua. It passes ventral to the M. neurocostomandibularis for most of its length. This insertion is just posterior to the insertion of the pars anterior on the ventrolateral surface of the bone at the level of the proximal end of the mandibular fossa.

5. M. mandibulotrachealis

The M. mandibulotrachealis of *Varanus* has been described by Sondhi (1958) as a delicate muscle arising from the anteroventral part of the mandible and extending posteriorly to divide into two parts. The dorsal part passes posteriorly dorsal to the tongue to insert on the lateral side of the trachea. The ventral part of the muscle extends posteriorly to fan out over the buccal floor near the insertion of the M. genioceratoideus, with an insertion on the ventral lining of the buccal floor. In *Natrix* (*Xenochrophis*), Sondhi (1958) found the origin to be similar to that of *Varanus*, with a medial bundle inserting on the trachea and a lateral bundle attaching to the lining of the buccal floor. It has not been reported for other genera.

This muscle is reported by Varkey (1979) for *Nerodia* as the M. geniotrachialis. It is a stout band of muscle that parallels the genioglossus. It originates at the anterior end of the dentary dorsal to the origin of the lateral genioglossus. It passes posteromedially to the tongue sheath and inserts on the ventral and ventrolateral surfaces of the first 14 tracheal rings.

6. M. neuromandibularis

The M. neuromandibularis has been described in detail by Sondhi (1958) for *Natrix* (*Xenochrophis*) and *Varanus*. In the latter it probably corresponds to the M. geniolateralis. Sondhi has described M. neuromandibularis as originating from the dorsolateral border of the middorsal aponeurosis and extending a short distance anterior along the dorsal side of the neck. The fibers divide into three sets, which pass into a common tendon inserting on the inner ventral surface of the skin. In *Natrix* (*Xenochrophis*) the origin is similar to that in *Varanus*. The insertion is on the ventromedial side of the posterior half of the mandible.

In some snakes the M. neuromandibularis arises from an aponeurosis at the middorsal line. In the anomalepidids, typhlopids, leptotyphlopids, uropeltids, and aniliids it inserts on the lower jaw. In the Xenopeltidae, Boidae, and other families it inserts on the raphe in common with the Mm. ceratomandibularis and costomandibularis.

7. M. costomandibularis

The M. costomandibularis has been described only for some snakes in which its origin is either from the cartilaginous ribs or the rib cage. In *Thamnophis* a medial slip originates from the peripheral surface of the lining of the pharyngeal floor and inserts on the common tendinous inscription of the M. neurocostomandibularis. In *Cylindrophis rufus* the insertion is on the second ceratobranchial as well as on the mandible.

8. M. constrictor pharyngis

The M. constrictor pharyngis of *Crocodylus* and *Gavialis* is a deeply laid transverse strap apparently restricted to the Crocodilia. Its origin is from the lateral surface of the cervical vertebrae and its insertion medial on the gular septum.

9. M. obliquus abdominis internus

Langebartel (1968) describes the M. obliquus abdominis internus as a trunk muscle of snakes, with an origin on the medial face of the ribs and an insertion on the linea alba.

10. M. transverse abdominis

Langebartel (1968) has also described the M. transverse abdominis as restricted to snakes and lying on the deep surface of the M. obliquus abdominis internus, with an origin on the medial face of the ribs. After extending posteriorly and medially, it inserts on the linea alba.

VI. The Tongue: External Morphology

The tongue of reptiles has been investigated by many workers, some of which are as follows: Gräper (1932), Nonoyama (1936), Gnanamuthu (1937), Oelrich (1956), Sondhi (1958), Avery and Tanner (1971), and Kroll (1973). Winokur (1974) published a major study on the adaptive modification of the buccal mucosae in turtles. His study is concerned not only with the tongue, but also with the glands found in the buccal area. Tongues in turtles vary in size and complexity (Fig. 22). Winokur states that

> Terrestrial herbivores (*Gopherus*, *Testudo*, and other tortoises) have the best developed mucous glands, whereas aquatic carnivores (*Chelydra* and *Chelus*) have few or no mucous glands.

In both *Chelydra* and *Trionyx* (Fig. 22 A, B) the tongue is without papillae or complex glands and is nonprotrusible, a characteristic of carnivorous chelonians. In *Trionyx* the short, rounded tongue is dorso-ventrally flattened and contains just a base and body. The base is formed from two posterior limbs that they enclose. Each basal portion extends anteromedially to unite in the tongue. Posterior to the tongue and glottis, the buccal-pharyngeal floor has numerous filiform papillae that Girgis (1961) has shown to have a respiratory function. The tongue of some, such as *Chelus*, has been developed as a lure in food-getting: the open mouth exposes a wormlike tongue structure to intice unsuspecting prey into the mouth.

In contrast, the terrestrial herbivorous chelonians (Tortoises; Fig. 22b) have a much larger lingual pad, which is glandular, fleshy, and somewhat protrusible. Tortoises have profuse lingual mucous glands on and between the lingual papillae as well as muscles capable of some lingual protrusion. They generally lack papillae posterior to the tongue.

Winokur (pers. comm.) considers *Dermatemys* (Fig. 22a) to be a special case. The tongue of this aquatic herbivore shows one end of the spectrum of buccal complexity in aquatic chelonians. Figures 22 and 23 illustrate the extremes seen between the tongues of aquatic carnivorous and terrestrial herbivorous chelonians. The tongue of *Dermatemys,* although proportionately smaller than that of terrestrial *Gopherus,* shows an extreme condition of buccal papillation, but one that is quite different from that of terrestrial herbivorous tortoises. Between these extremes are the majority of chelonians, such as *Pseudemys,* which tend toward omnivorousness.

The tongues of *Alligator, Crocodylus,* and *Gavialis* lack any specific areas identifiable as base, body, or apex. The tongue is a mass of tissue between the mandibular symphysis and glottis attached to the lining of the buccal floor except at its anterior tip. It can be elevated and depressed, but not protruded.

Sauromalus (Fig. 24) and *Brachylophus* (Fig. 25) show generalized lizard tongues, with their extensive papillation and lateral extensions on each side of the glottis. Such tongues are protrusible and obviously serve a masticatory function. In *Amblyrhynchus, Brachylophus, Conolophus, Ctenosaura, Cyclura, Dipsosaurus, Iguana,* and *Sauromalus* the tongue is well developed and large. In the above genera it is cleft anteriorly, with the most anterior tips lacking papillae. There is a smooth pad ventral to the tips (Fig. 24).

In the teiid *Ameiva* the tongue is rounded and slightly notched posteriorly and covered by a lingual sheath. It bears a deep terminal notch anteriorly that separates the tapering elongate terminal prongs. A lingual sheath is absent in *Cnemidophorus* and other macroteiids. The tongue of *Cnemidophorus* (Fig. 26) represents a moderate advancement in the development of flexibility, and *Chamaeleo* (Fig. 27) is a highly specialized free tongue.

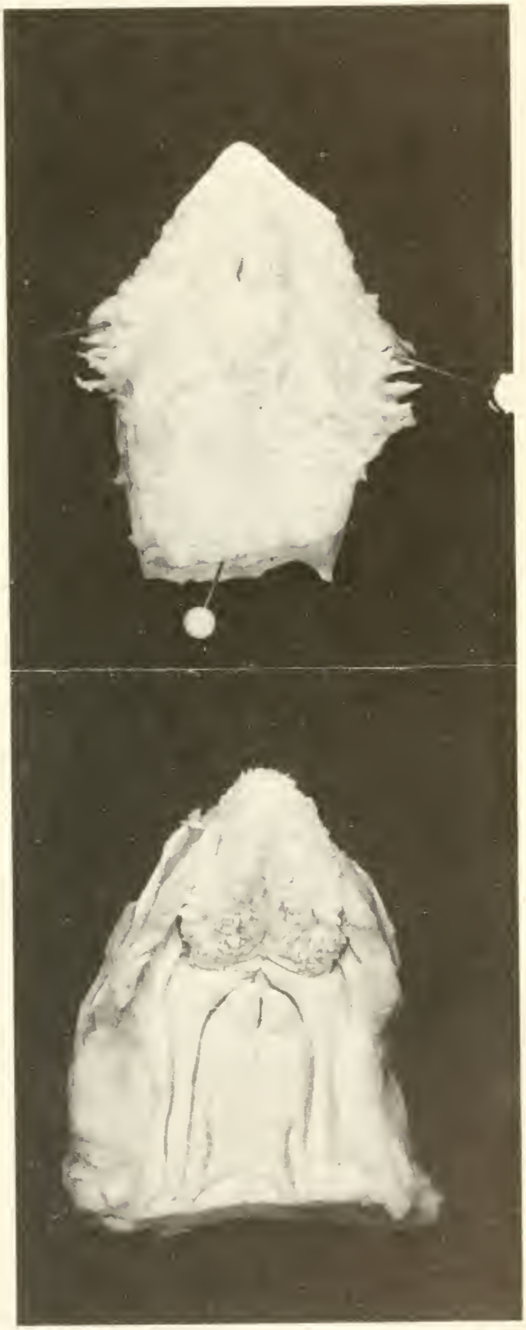


Fig. 22. Tongue size as indicated in: A, *Dermateys mawi* (UU 9845), above; B, *Gopherus* (UU 5961), below. It should be noted that the glottis is moved caudad as the tongue increases in size. Photographs provided by Robert M. Winokur.

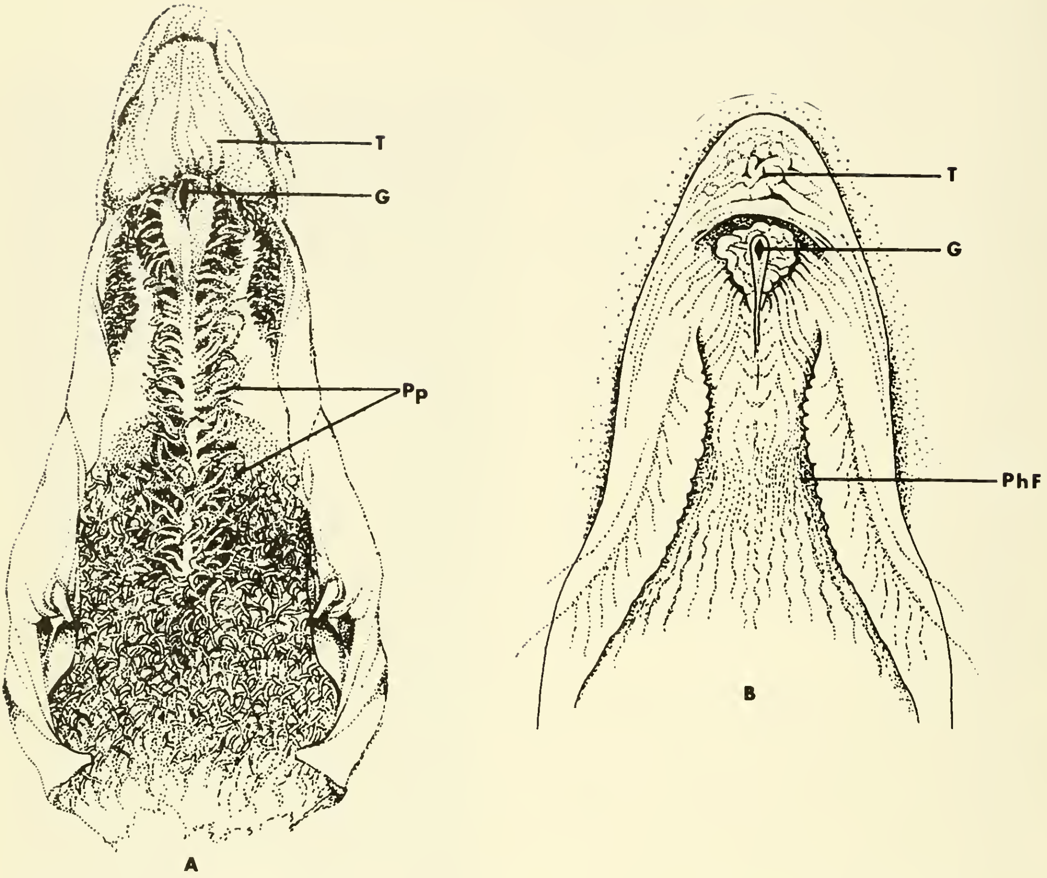


Fig. 23. Tongue of *Trionyx spiniferus*: A, showing its position in relation to the glottis and pharynx area with its filamentous papillae; B, *Chelydra serpentina* showing the nonpapillated pharynx.

In *Lanthanotus* the tongue is deeply incised terminally, forming two tapering prongs. The anterior half of the tongue is elongate, narrow, smooth, and elastic, whereas the posterior half is wide and covered with papillae. In *Shinisaurus* the tongue is similar, but the posterior half is more triangular and the terminal prongs are not as well developed. *Heloderma* has a similar tongue but with proportionately longer terminal prongs than in the latter.

The tongue of *Varanus* is elongated and protrusible, terminating in a forked tip anteriorly. The entire median part of the buccal floor is occupied by its mass. Posteriorly it extends as a bifurcated portion on each side of the glottis and esophagus and into the neck proper. Sondhi (1958) considers the tongue to be divisible into three parts: the base which is bifurcated; the body, formed by the union of two basal masses of muscle; and lastly the apex, consisting of a pair of prongs. Each muscular mass forming the basal branch of the tongue arises on the distal end of the second ceratobranchial as a slender longitudinal M. hypoglossus, which extends along the ventrolateral surface of each ceratobranchial to pass obliquely to the dorsolateral side of the neck. This muscle eventually occupies a midventral position, with the middle of its basal branch lying ventromedial to the point of articulation between the distal and proximal portions of the second ceratobranchial. Its anterior portion lies ventrolateral to the proximal piece of the anterior cornu at the point of articulation with the basihyoid.

As the two basal branches of the tongue approach, they become thick and subcylindrical and eventually lie dorsal to the basihyoid and ventral to the portiones pro-

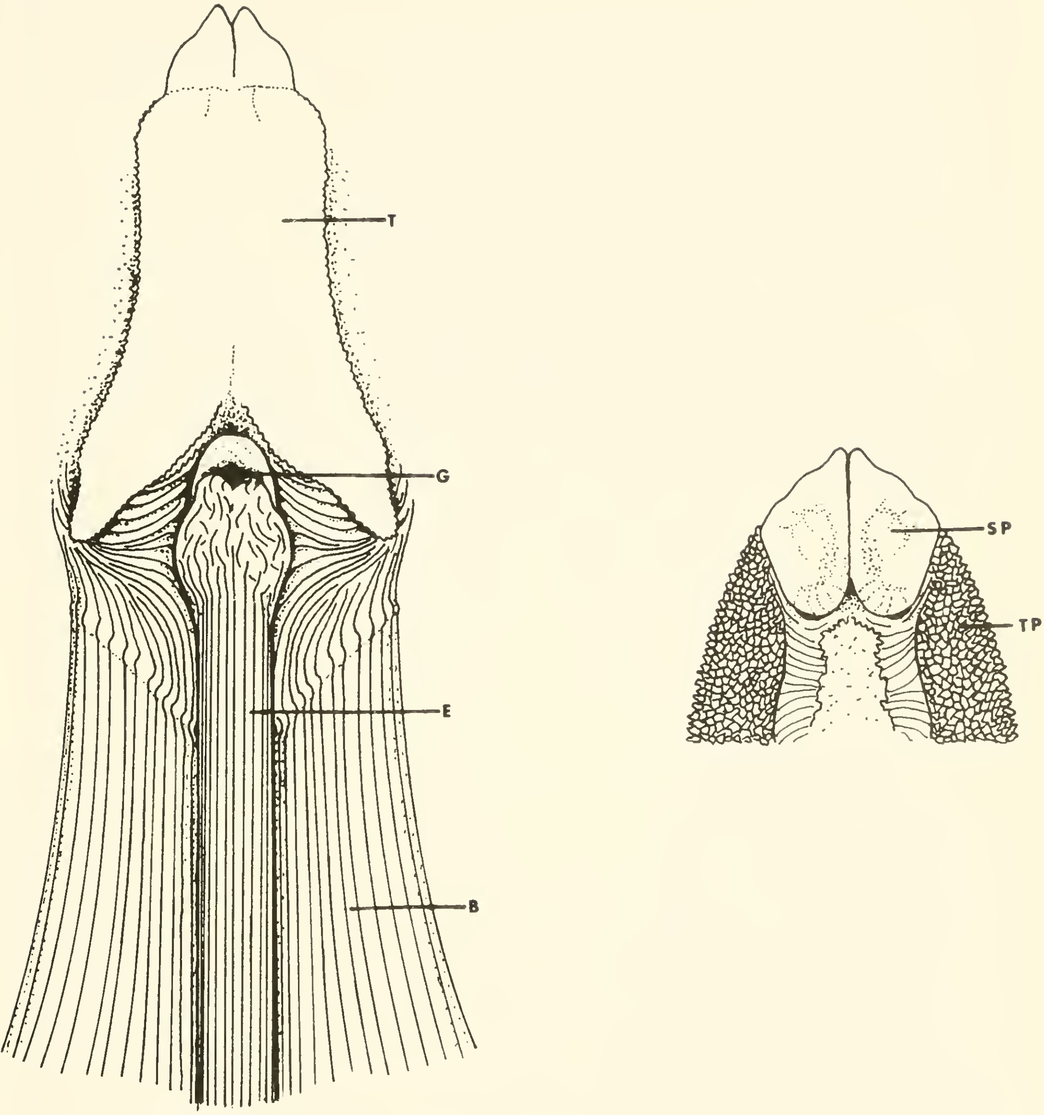


Fig. 24. Tongue of *Sauromalus obesus*: A, outline of dorsal view; B, ventral view showing the smooth pads surrounding the tips. (Dorsal surface as in *Brachylophus*, Fig. 25).

ximales of the anterior cornua. At their anterior extremes the two branches are enclosed in a lingual sheath, where they unite to form the body of the tongue. The body is enclosed by the lingual sheath and occupies the medial area of the buccal floor. Ventrally the anterior end of the lingual process lies inside the lingual sheath and opposite the glottis. Also, ventrally the two handlelike pieces of the portiones proximales overlap medially to cover the body of the tongue. The apex of the tongue consists of a pair of prongs, rounded, thick at the base, and tapering to pointed ends anteriorly.

We recognize at least three types of saurian tongues. First, in the generalized tongue, seen in such forms as *Sauromalus* and *Coleonyx*, the dorsal surface is papillate and highly glandular; although the tip is divided, it is not extended into a pair of elongated prongs. Second, an elongate, narrow tongue with a pair of elongate prongs occurs in such groups as the teiids and varanids. In these lizards with deeply incised tips, the tongue is narrow and glandular and serves not only the purpose of mastication, but also functions as a sensory organ. Sondhi (1958) implies that such tongues are closely related anatomically to the tongues of snakes, and he compares the tongue of the natricine snakes to that of *Varanus*. Third, an entirely different tongue is found in *Chamaeleo*. Instead of a further development of the tip as in *Varanus*, the chamaeleonids have developed a blunt end with a highly glandular anterodorsal surface used in capturing and ingesting food.

In snakes the tongue has developed a greater bifurcation with filamentous lateral projections on each fork. Such tongues are sheathed at their base and function as a sensory rather than a masticatory or food-getting organ. Our understanding of lingual structures and the associated buccal mucosae, however, is still sketchy and much comparative study must be done before an adequate understanding of their anatomy is available.

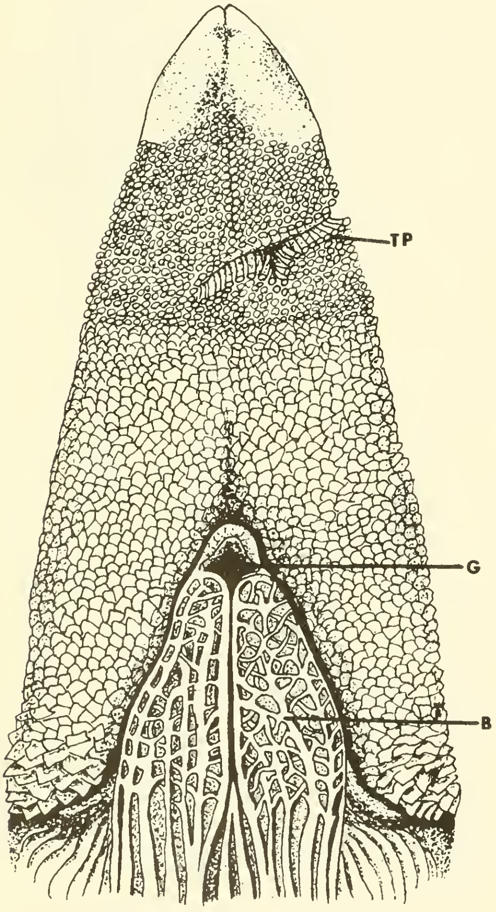


Fig. 25. Tongue of *Brachylophus* showing the size and nature of the tongue papillae (TP), and the reticulated, ridged nature of the tissue (B) extending posterior to the glottis (G).

In *Natrix* (*Xenochrophis*) Sondhi (1958) also describes the tongue as having three parts, with the basal branches lying parallel on each side of the midlongitudinal line ventral to the trachea. Each branch passes anterior to the second ceratobranchial ventromedially. As they approach the dorsal part of the basihyoid, the two branches unite to form the body of the tongue, which is elongated and compressed dorsoventrally. In the retracted position the tongue is almost entirely encased by the lingual sheath dorsal to the basihyoid and lingual process and ventral to the trachea. The apex of the tongue is broad at the base but tapers anteriorly.

The tongue has a variety of forms, sizes, and functions in reptiles. In some aquatic turtles it is a small pad rather tightly applied to the floor of the anterior part of the mouth. Such tongues are nonprotrusible and actually have a very limited ability to move. In most chelonians, except for some aquatic turtles and crocodilians, the tongue is more than a pad and serves many useful functions. In some chelonians (*Gopherus*, Fig. 22b), most lizards (iguanids and agamids for example, Fig. 24), and in the more primitive Sphenodontidae the tongue may serve a masticatory function. It is a "food-getting" organ in the "free"-tongued Chamaeleonidae and has a sensory function in snakes and some lizards.

As noted above, the degree of flexibility in the tongues of reptiles varies from little to considerable movement. Because tongues in most reptiles (except snakes) are associated with feeding, that is, ingestion, their anatomy and perhaps the degree of flexibility is dependent on adaptive change to meet such activities.

In the Sphenodontidae and Chamaeleonidae the extremity is very blunt (Fig. 27). The *Chamaeleo* tongue and its associated muscles and other tissues may be as long or longer than the body when fully extended. A broad fleshy tongue with smooth and papillate areas is seen in the gekkonids and iguanids (Figs. 24, 25). The Testudines and

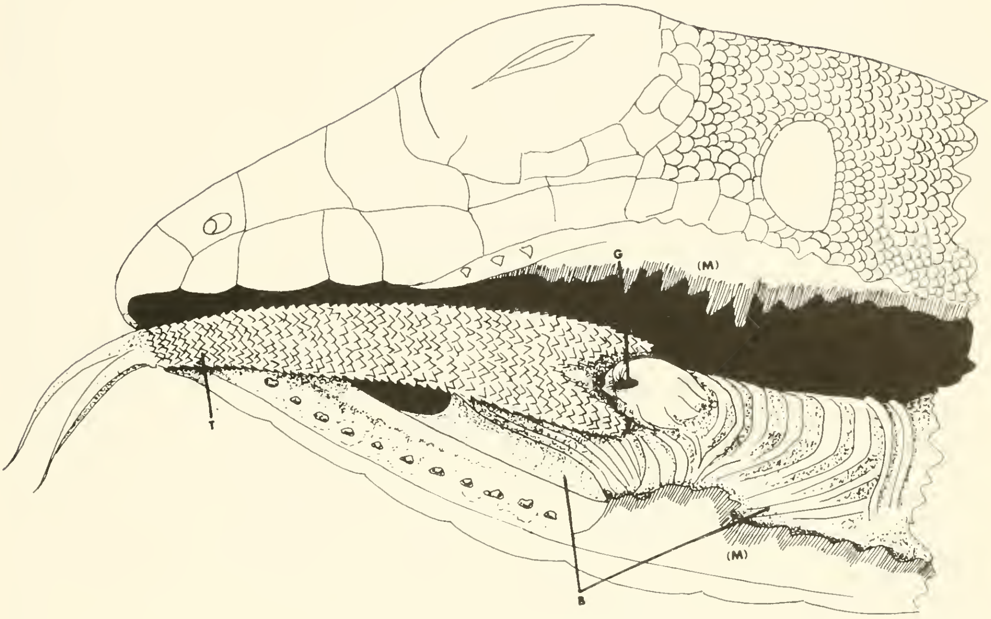


Fig. 26. Dorsolateral view of *Cnemidophorus tigris* (BYU 17366) showing the forked tongue and the narrow papillate body of the tongue (B), floor of the mouth (M), cut muscles.

Crocodilla may have small pads with little movement or, as in those such as *Gopherus*, the tongue is larger, fleshy, and closely tied to the buccal floor and has varying protrusibility.

The highly flexible and protrusible tongue of snakes has become an elongate, slender, sensory organ. In this form it has changed to an entirely different organ than that of most other reptiles, in which the tongue is an organ lying on the buccal floor. In its normal position it is sheathed, with little or none of it visible on the buccal floor. Also, the opening of the tongue sheath has moved anterior so as to lie just posterior to the mental synthesis, with the glottis immediately posterior to the sheath opening. Although ophidian tongues are structurally and functionally quite different from those of most other reptiles, they are nonetheless developed phylogenetically from the same basic structures. The adaptive changes found in the tongues of reptiles are probably some of the most remarkable to be found, for one organ, in the vertebrate series.

VII. MUSCULATURE OF THE TONGUE

The tongue is associated with musculature of two basic types: (1) extrinsic musculature, which does not contribute to the structure of the tongue itself, and (2) intrinsic musculature, which makes up the lingual structures.

1. Extrinsic musculature

In most reptiles the M. geniohyoideus is the primary extrinsic muscle of the tongue. It is paired and arises from the mandibular symphysis to insert on the external part of the M. hypoglossus, parts of the hyoid apparatus, or the lining of the buccal floor. In *Sphenodon* it has two extensions, one dorsal and one ventral.

In the turtles *Trionyx* and *Lissemys* the M. geniohyoideus is undivided and broad. It originates on the mandibular symphysis and extends posteroventrally to insert on the fascia of the ventrolateral border of the body of the tongue.

The M. geniohyoideus of *Alligator* takes origin from the mandibular symphysis and di-

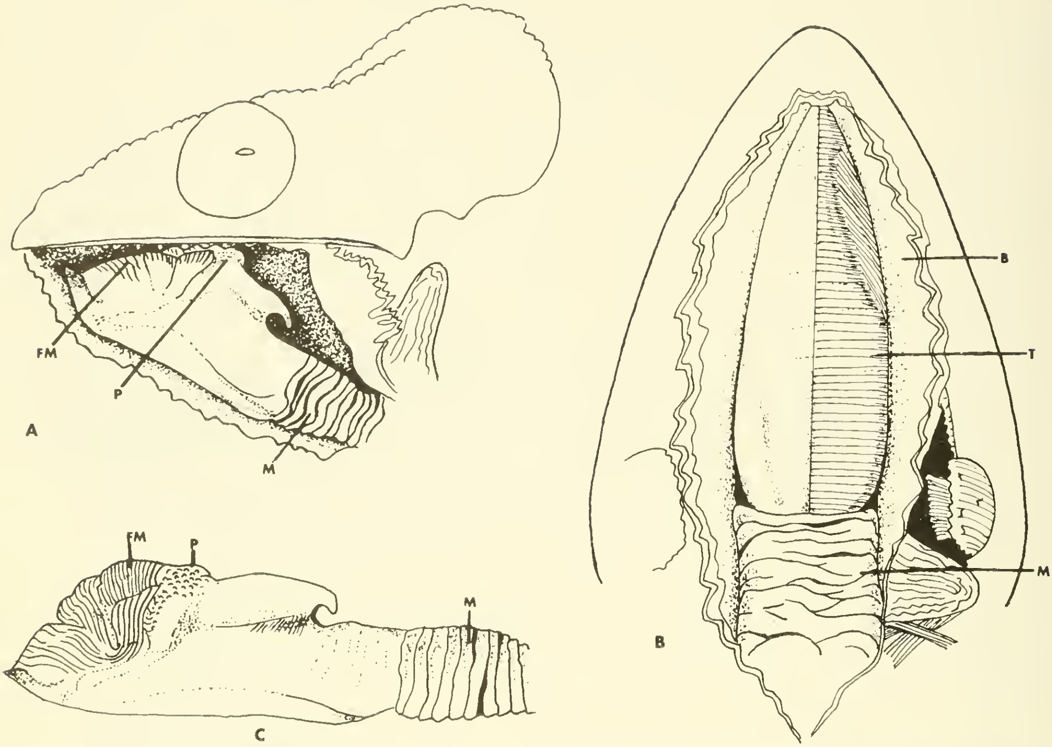


Fig. 27. Tongue of *Chamaelon brevicarnis*: A, lateral view showing position of tongue in mouth cavity; B, ventral view with muscles and other tissues removed to show the tongue and the folded M. hypoglossus; C, tongue removed, lateral view (BYU 12422).

vides into medial and lateral bundles. The medial bundle is narrow and interdigitates with its opposite member to insert on the basihyoid. The lateral bundle is broader and inserts on the tongue. The M. geniohyoideus of *Crocodylus* arises from the mandible and divides into two lateral bundles, both of which extend posterodorsal to where the median bundle of the M. geniohyoideus inserts on the anterior border of the hyoid. The lateral bundle inserts on the anterior and ventral border of the anterior cornu. In *Gavialis* the M. geniohyoideus has portiones minor and major, with the portio minor being slender and originating with the mandibular symphysis. It extends caudad to insert on the ventral part of the M. hyoglossus. The broader portio major lies lateral to the M. hypoglossus, takes origin from the mandibular symphysis dorsal to the portio minor, and extends obliquely caudad to a fanlike insertion on the fascia near the middle of the M. hyoglossus (Sondhi 1958).

In *Hemidactylus* the M. geniohyoideus is well developed, with insertions on the ventrolateral surface of the tongue and the hyoid cornu. In *Anolis, Sitana, Calotes,* and *Draco* the M. geniohyoideus fans out to insert on the buccal floor, with the main body attaching to the sides of the second cornu and the first ceratobranchial. The M. geniohyoideus of *Mabuia* covers the M. hypoglossus on its lateral surface, whereas in *Cabrita* it originates on the medial sides of the mandible. The muscle extends posteriorly to insert on the lining of the buccal floor. In the area of the glottis the main bundles of the M. geniohyoideus divide into two and insert on the first ceratobranchial on the ventral side of the M. hypoglossus.

The M. geniohyoideus of *Chamaeleo brevicornis* consists of two main bundles: the dorsal one inserts on the buccal floor, the ventral one on the body of the hyoid and the first ceratobranchial, lacking any connection with the tongue. The dorsal bundle has three slips that insert (1) on the side of the pouch in the buccal floor where the tongue retracts, (2) on the buccal floor two-thirds the length of the jaw, and (3) after extending obliquely under the second bundle, on tissue lateral to that bundle.

In *Varanus* the M. geniohyoideus, according to Sondhi (1958), can be divided into two parts. The Mm. geniohyoidei portio minor is very short, extending obliquely posteromedially to insert on the anterior part of the lining of the buccal floor near the midline, and the M. geniohyoideus portio major extends posteriorly for a much longer distance to meet its opposite member at the midline. As the two muscles lie together at the midline ventral to the tongue, each separates into a dorsal and ventral sheet. Each of these divisions insert on the ventral, lateral, and dorsal sides of the tongue to attach on the fascia of the basal branch of the tongue. In *Varanus indicus* the main body of the M. geniohyoideus inserts in a fascia in common with the M. sternohyoideus and to the first ceratobranchial, which lies immediately deep (dorsal) to the fascia.

The M. geniohyoideus of the iguanid lizards *Amblyrhynchus*, *Brachylophus*, *Chalarodon*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, *Oplurus*, and *Sauromalus* extends posteriorly from the ventromedial surface of the mandibular rami and divides into medial and lateral bundles. The medial bundle passes posteriorly to insert on the ventral surface of the first ceratobranchial. The lateral bundle inserts on the ventrolateral surface of the first ceratobranchial, lateral to the medial bundle. It lies ventral and lateral to the anterior part of the M. hypoglossus. Oelrich (1956), in describing the condition in *Ctenosaura*, states:

> The lateral group twists so that at its origin the ventral surface is medial and the dorsal surface is lateral, the most lateral fibers extending dorsally and inserting laterally. The more medial fibers fan out and insert all along the ventrolateral surfaces of the tongue to its posterior end, interdigitating with the dorsal transverse fibers of the intrinsic tongue musculature.

The M. geniohyoideus of snakes is long and slender with one or more heads of origin. In *Liotyphlops* it arises as two heads, but in the Typhlopidae as a group its origin is from the inter-ramal connective tissue. In the Leptotyphlopidae the origin is by a single head or tendon from the dentary. *Rhinophis* (Uropelitidae) has a medial head originating on the inter-ramal pad, but in *Platyplecturus* only the lateral head is present. *Cylindrophis*, *Sanzinia*, *Enhydris*, *Aipysusus*, and *Bothrops* all possess a M. geniohyoideus with a single head. In most cases the M. geniohyoideus is bound to the tongue by a sheath and extends with the tongue at least to its base. In some forms such as *Liasis*, *Eryx*, and *Xenopeltis* the fibers extend even farther to insert on the M. hyoglossus.

In *Atretium* the M. geniohyoideus resembles that of *Varanus*, with three divisions: lateral, ventral, and dorsal. Each of these originates on the inter-ramal pad. The lateral division has two bundles, one of which extends dorsolaterally to interdigitate with fibers of the second bundle. Together these bundles insert on the lining of the buccal floor. The ventral division extends posterolaterally to separate into medial, inner, and a lateral bundle in the area of the glottis. The lateral group of fibers cross the medial ventrally to pass medially and to unite with the dorsal division of the M. geniohyoideus. The medial fibers extend posteriorly along the trachea to fan out and insert on the buccal floor, with the main bundle inserting on the trachea itself. The fibers comprising the dorsal division of the M. geniohyoideus extend posteriorly to insert on the lining of the buccal floor. The remainder of the muscle extends posteriorly to join with the lateral bundle of the ventral division and pass parallel to the M. hyoglossus and insert into the tongue as a tendon.

The M. geniohyoideus of *Natrix* arises from the inter-ramal ligament and consists of the M. geniohyoidei portiones minor and major. The portio major consists of fibers similar in configuration to the lateral bundle of the ventral division of *Atretium*. The medial bundle is not connected to the hyoid and may be a separate muscle, the M. mandibulotrachealis as described in *Natrix* by Sondhi (1958). The portio major is similar to the dorsal division of *Atretium*, although its fibers do not insert on the buccal floor. The short, slender portio minor extends posteriorly to insert on the anterior buccal floor. Its origin is adjacent to that of the portio major. The portio major is long, and its fibers converge posteriorly to insert on the base of the tongue.

2. Intrinsic Musculature

The anatomy of the tongue is poorly understood except in a few types that have been studied in detail. Attempts at explaining its morphology in *Ctenosaura* by Oelrich (1956) and *Varanus* and *Natrix* by Sondhi (1958) have only indicated the complexity of this structure in reptiles. The simplest interpretation is that the tongue of reptiles consists of a single muscle, the M. hyoglossus, which has been modified to serve many complex functions.

In the Crocodilia the tongue lacks the recognizable complex of intrinsic muscles seen in many and is formed from a more simplified association of the fibers of the hyoglossus, which originates on the second ceratobranchials and inserts on the buccal floor. The tongue of *Alligator* has medial fibers of the M. hyoglossus that cross to opposite sides and interdigitate with fibers opposite the muscle. In *Crocodylus* the M. hyoglossus has a triple origin with fibers from the outer proximal part of the second ceratobranchial, the ventral area of the second ceratobranchial at its point of articulation with the basihyoid, and the tendinous sheet where sternohyoid fibers insert on the articulation of the second ceratobranchial with the basihyoid. The tongue of *Gavialis* is described by Sondhi (1958) as having a M. hyoglossus with a double origin. One head originates as a tendon from the middle of the ventral border of the second ceratobranchial, and the second head originates near the point of articulation between the second ceratobranchial and the basihyoid. The M. hyoglossus extends anteromedially with interdigitations of fibers from both sides as the muscle inserts on the lining of the buccal floor.

The tongue of *Lissemys* is formed by a M. hyoglossus consisting of two bundles each originating on the proximal portion of the second ceratobranchials (Gnanamuthu 1937). One bundle inserts on the side of the lingual process, and the other extends anteriorly to divide into two bundles to form the body of the tongue. In *Trionyx* the M. hyoglossus differs from that of *Lissemys* in that it is a single muscle as in *Varanus* and *Natrix*. The origin is from the ventral surface of the proximal part of the second ceratobranchial in the form of longitudinal fibers. These extend anteriorly and are surrounded by a sheath of connective tissues. As the muscle passes anteriorly, the fibers split into three longitudinal bundles: outer, middle, and internal. This division occurs anterior to the union of the two basal branches of the tongue.

Sondhi (1958) describes the tongue of *Varanus*, using a series of successive transverse sections. To summarize his description, the longitudinal fibers of the M. hyoglossus become oblique and then transverse, with more and more longitudinal fibers changing direction at the periphery of the tongue. The main muscular mass differentiates into two sets of fibers: one peripheral with circular fibers (pars externa) and one inner with longitudinal fibers (pars interna). The two groups are separated by a thin fascial capsule.

The circular fibers of the pars externa become tangential and interweave before the basal branches of the tongue combine at their dorsal borders. At the same time, the fibers in different areas of the pars externa change directions to form three intrinsic muscles: the Mm. verticalis linguae, transversalis linguae, and longitudinalis linguae. The M. verticalis linguae is composed of circular fibers of the pars externa on the inner side of each basal branch of the tongue, which extend vertically to lie between the remaining bundles of the pars externa. The dorsally dispersed fibers of the right and left pars externae become continuous at the union of the two basal branches of the tongue to form the M. transversalis linguae. Posterior to the union of the two basal branches the M. longitudinalis linguae is formed from fibers of the M. transversalis linguae, along the dorsal branch of each half of the tongue, which change their direction from circular to longitudinal. Several bundles of these fibers merge together to form a mass on the dorsolateral side of the tongue, which extends anteriorly to the apex. Just posterior to the anterior bifurcation of the body of the tongue, the pars interna of the M. hyoglossus on each side bifurcates to form two portions, which are separated by some of the bundles and the M. verticalis linguae.

Each prong terminates with the diminishing of the longitudinal and circular bundles and the insertion of their obliquely directed fibers on the epithelium of the tongue.

Natrix (*Xenochrophis*) has been described by Sondhi (1958) as having a M. hyoglossus similar to that of the lizard *Varanus.* In *Natrix* the M. hyoglossus envelopes the second ceratobranchial at each side of the origin. Unlike that in *Varanus,* the M. hyoglossus of *Natrix* becomes ventromedial to the ceratobranchial and combines with its opposite member far posterior to the basihyoid. The M. hyoglossus also divides into parts externa and interna, but in the substance of the tongue rather than at its base as in *Varanus.* A number of longitudinal fibers of the M. hyoglossus separate from the rest of the pars externa at the periphery of the tongue to form the partes externa and interna. This change in direction of the fibers is directly associated with the formation of the Mm. verticalis linguae, transversalis linguae, and longitudinalis linguae the same as in *Varanus.* The only difference is that the fibers of the M. longitudinalis linguae are formed more anteriorly in the body of the tongue in *Natrix* than in *Varanus.*

Varkey (1979) describes the tongue of *Nerodia cycloprion* as being formed of intrinsic tongue muscles and the M. hyoglossus. He describes the M. hyoglossus as long, slender, paired retractor muscles making up the bulk of the tongue. They arise from the medial edge of the posterior tips of the ceratobranchials of the hyoid, pass rostrally, laterally, and ventrally to the intrinsic tongue muscles, and are pressed so closely together with them as to be almost indistinguishable. The hyoglossus muscles attach to the hyoid cornua, the tongue sheath, the oral ·mucosa, the fascia medial, and just posterior to the lateral sublingual glands.

The intrinsic musculature of the tongue of *Lichanura roseofusca* has been described by Hershkowitz (1941) as consisting of five distinct bundles. In the posterior part of the tongue all but the M. verticalis are present. The M. transversus inferioris forms a sheet on the ventral side of the tongue extending dorsally along the lateral side to meet the ventral extension of the M. transversus superioris.

The M. transversus superioris occupies most of the dorsal part of the tongue deep to the superficial muscle, the M. lingualis, which is restricted to the most dorsal muscular layer of the free, unforked part of the tongue.

The M. verticalis forms a midsaggital lingual septum, thin toward the anterior and thick at the posterior end. The fibers of the M. verticalis run at right angles to those of the Mm. t. superioris and t. inferioris. Dorsally its bundles interweave with those of the M. lingualis.

The ceratoglossus muscles form a pair of central muscles extending the entire length of the organ and forming most of the cross section of the tongue.

Posterior to the bifurcation of the tongue into terminal prongs, the Mm. verticalis linguae and transversalis linguae intersect at right angles. Thus, in section the tongue can be divided into four quarters composed of bundles of the M. longitudinalis linguae and the pars interna.

At the anterior tip of the tongue, a dorsal and a ventral notch occur medially. The dorsal notch deepens to separate the bases of the terminal prongs. At this point the bundles of the M. longitudinalis linguae of each side divide into smaller bundles and intermingle anteriorly toward the tips of the prongs to terminate in the connective tissues of the lingual epithelium (Fig. 26).

The M. hyoglossus in *Chamaeleo brevicornis* originates on the tip of the distal end of the first ceratobranchial. A small cartilaginous knob on the end of the ceratobranchial, which appears to be a remnant of the epibranchial, also serves as a point of origin for many fibers. The first and second cornua extend anterolaterally from the basihyal; therefore the M. hyoglossus, in its contracted position, extends from its origin medially to the lingual process, where it makes a right angle turn to follow the lingual process into the tongue and to its insertion in the connective tissue surrounding the tongue. Upon reaching the tongue, the M. hyoglossus divides into the two sections described by Sondhi (1958) as the pars externa and a medial longitudinal part, the pars interna. A series of circular fibers, which are a part of the sheath,

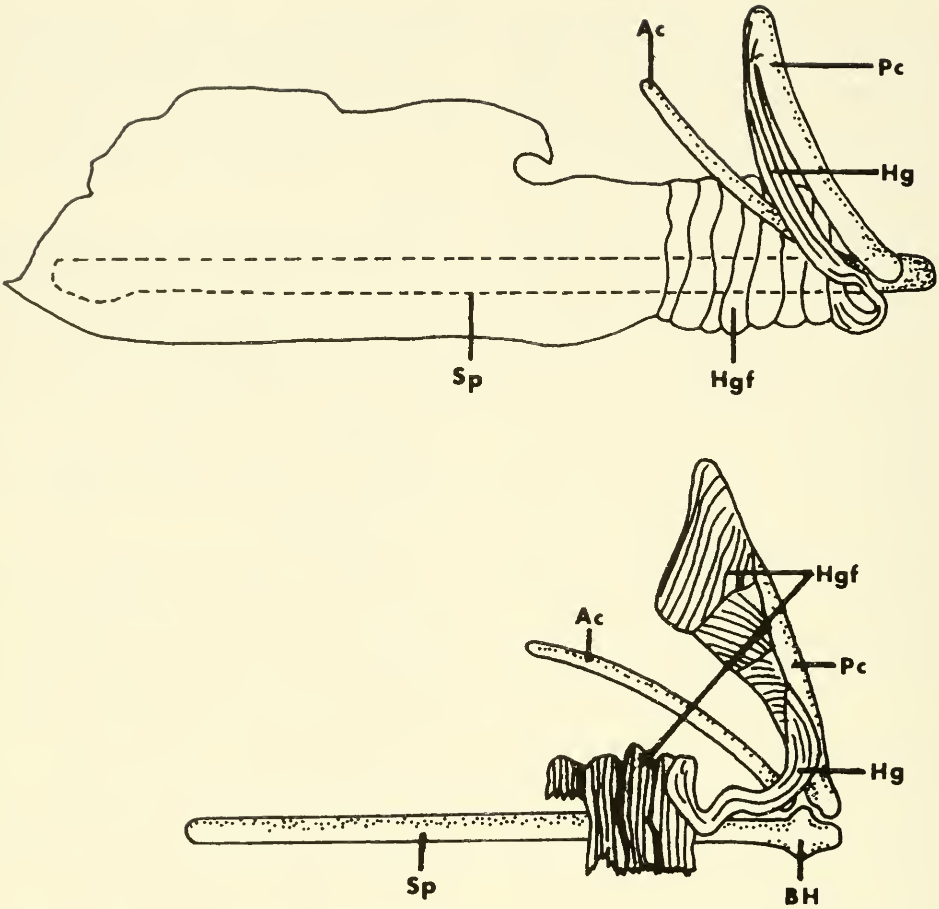


Fig. 28. Lateral view of the tongue of *Chamaelon brevicarnis* showing M. hypoglossus from its origin on the posterior cornu to its folds before entering the tongue (BYU 12422).

surrounds the basal part of the tongue as a transverse sheet and encloses the distal lingual process and inserts dorsally into the tongue.

In *Chamaeleo* the M. hyoglossus is folded, less so from its origin to the angle formed at its median posterior than as it extends along the lingual process (Fig. 28). The folds are deep and number 10 before the muscle enters the tongue. When fully extended, this folded part becomes an elongate, slender shaft supporting the clublike tongue. Gnanamuthu (1930) described the anatomy and function of the hyoid apparatus and tongue in *Chamaeleo cacaratus.* His figures 5 and 6 correspond closely to our findings in *Chamaeleo brevicornis.* The folding is similar to the folds in the bellows of an accordian, whereas the muscular folds in free-tongued plethodontid salamanders is a series of looped folds (Tanner 1952).

The outer bundle further divides into five to six smaller bundles, which lie beneath the dorsolateral border of the tongue to form the M. longitudinalis linguae. The fibers of the upper dorsolateral bundles of the M. longitudinalis linguae extend anteriorly to become obliquely transverse and give rise to the M. transversalis linguae, with the lower bundles continuing longitudinally to merge with each other. The internal longitudinal fibers of the M. hyoglossus become compact and vertical to form the M. verticalis linguae, just behind the tip of the tongue. At that point the middle bundle, between the Mm. transversalis linguae and verticalis linguae, passes dorsally so as to lie above the latter two bands. In the terminal end of each muscular

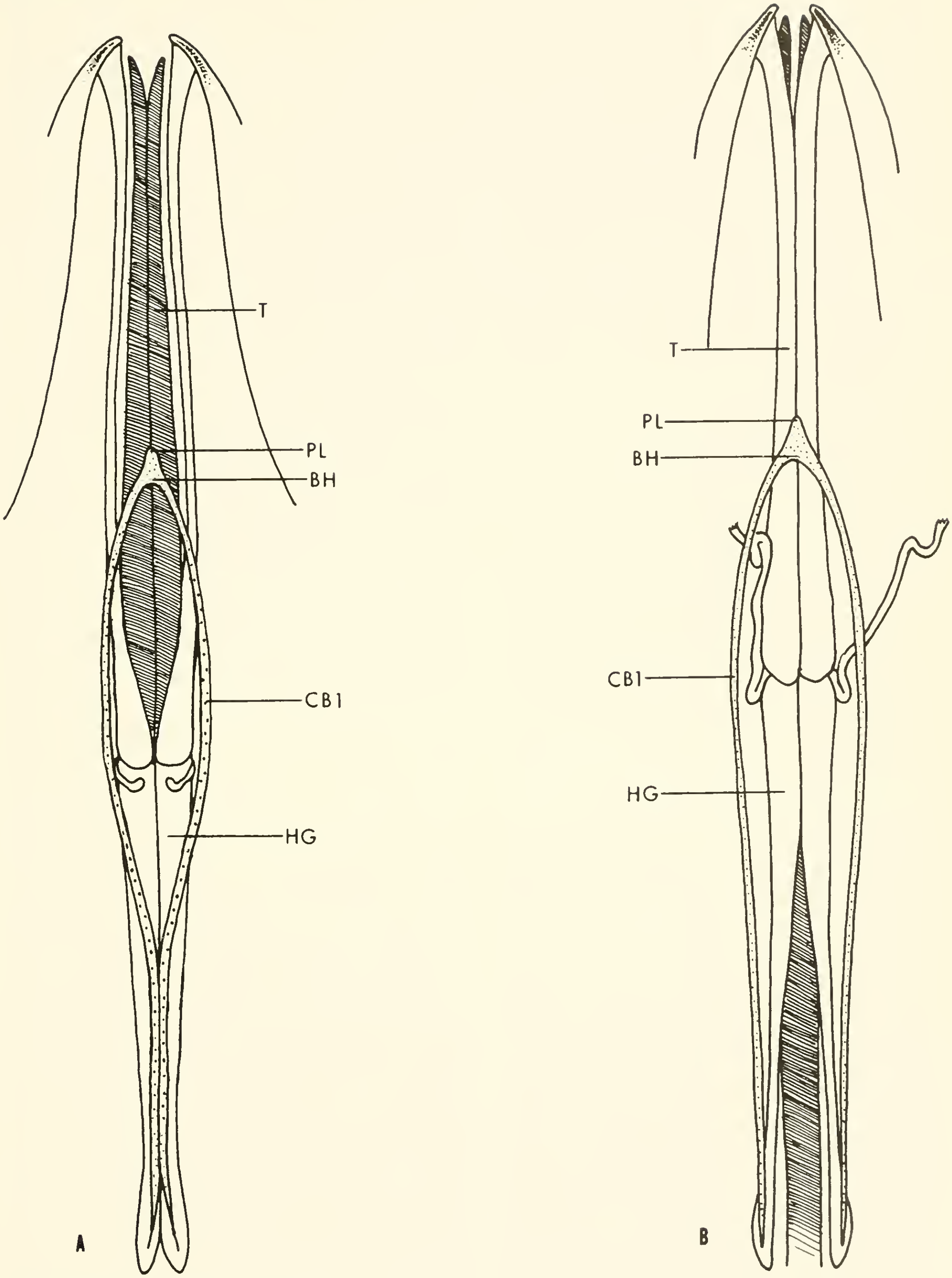


Fig. 29. Ventral view of hyoid apparatus and associated structures: A, *Crotalus v. lutosus*; B, *Pituophis m. deserticola.* HG—m. hyoglossus, t—tongue.

prong extending into the tongue from each side, the various bundles dwindle and insert in the subepithelial connective tissue of the tongue.

In Figure 29 the general structural relationships of the hyoid, tongue and M. hyoglossus are depicted for the genera *Crotalus* and *Pituophis*.

In summary, the intrinsic muscles of the tongue are actually fibers of the hyoglossal muscles that extend in varying directions. Unfortunately, the remainder of our knowledge of the tongue and related structures is incomplete. Many structures such as lingual glands, glottis, trachea, and their associated muscles and nerves have not been fully investigated in all groups. Zug (1971) has studied the arterial patterns in iguanids, Winokur (1974) has studied the buccal mucosae in turtles, and Schumacher (1973) has examined the hyolaryngeal muscles and skeleton in turtles and crocodilians.

VIII. Innervation of Buccal Floor Musculature

A. General

The innervation of muscles in reptiles has been generally neglected, and for this reason it is difficult to homologize their detailed musculature. Detailed descriptions of the nerve patterns in the buccal floor of reptiles are available from the following workers: Osawa (1898), Watkinson (1906), Reese (1915), Willard (1915), Poglayen-Neuwall (1953, 1954), Oelrich (1956), Schumacher (1956, 1973), Sondhi (1958), and Rieppel (1978, 1981). Soliman (1964) describes and figures the nerves in the head of *Chelydra serpentina* and provides colored plates depicting the nerves entering the muscles associated with the buccal floor and the tongue. Islam (1955) and Islam and Ashig (1972) describe the cranium and cranial nerves of *Uromastyx hardwicki*, and Renous-Lecru (1972) discusses the branchial plexus in *Agama* and *Chalarodon*.

All these workers indicate that in reptiles the IXth (glossopharyngeal), Xth (vagus), XIth (spinal accessory), and XIIth (hyoglossal) cranial nerves usually occur in close association and form a glossohyoidean plexus. Some uniformity does exist in the innervation of the throat muscles of reptiles, as demonstrated by the fact that in all reptiles the Vth (trigeminal) cranial nerve innervates the M. mylohoideus anterior, the VIIth (facial) innervates the Mm. mylohyoideus posterior and constrictor colli, and the XIIth (hypoglossal) and anterior spinal nerves innervate the M. constrictor colli.

B. Cranial Nerves

Oelrich (1956) presented a clear picture of the pattern of cranial nerves in the iguanid *Ctenosaura*. He found the following nerves innervating muscles of the buccal floor. A similar pattern in all cases has been described for *Anolis* by Willard (1915), for the trigeminal in turtles by Poglayen-Neuwell (1953), and for *Varanus* by Watkinson (1906).

1. *N. trigeminus*: A branch of the trigeminal nerve (ramus ad musculum mylohyoideum) passes through the posterior mylohyoid foramen to enter the lateral fibers of the first mandibulohyoid muscle and terminates anteriorly on the M. intermandibularis posterior. A second branch, the anterior mylohyoid nerve, emerges on the medial side of the mandible from the anterior mylohyoid foramen of the splenial bone to pass over the M. mandibulohyoideus I to enter the ventral surface of the M. intermandibularis anterior. A section of the mandibular ramus continues anteriorly to the lingual ramus of the hypoglossal nerve, where the latter passes through the anterior inferior alveolus foramen of the dentary to divide into two branches. The anterior glandular branch passes the ventral surface of the M. intermandibularis anterior, whereas the posterior branch enters the Mm. intermandibularis anterior and genioglossus.

2. *N. facialis*: The facial nerve divides into a hyoid ramus that innervates a part of the M. intermandibularis that inserts on the retroarticular process of the mandible. It also innervates the M. constrictor colli and the posterior border of the M. intermandibularis.

3. *N. glossopharyngealis*: The M. hyoglossus is innervated by a ramus formed from branches of the glossopharyngeal and hypoglossal nerves.

4. *N. hypoglossalis*: There are four small ventral branches of the hypoglossal nerve that innervate the M. mandibulohyoideus I. The hypoglossal divides into three main branches at the point where the Mm. genioglossus and hyoglossus join. These branches include the ramus lingualis lateralis, which extends anterolaterally to enter the insertion of the M. genioglossus and medial and lateral areas of the M. genioglossus. It next emerges to join the lingual ramus of the trigeminal

nerve, which then enters the tongue. The remaining two branches, intermedialis and medialis, go directly to the tongue, where they innervate its musculature.

Watkinsón (1906) described the nerve patterns seen in *Varanus* and found the following:

a. *N. trigeminus*: There are three main branches of the trigeminal nerve (rami opthalmicus, maxillaris, and mandibularis); however, only the ramus mandibularis goes to the buccal floor, where it has three branches.

The first branch, the ramus ad musculum mylohyoideus, originates from that part of the ramus mandibularis (portio alveolaris inferior) that lies within the alveolar surface of the dentary. It emerges to proceed posteriorly, with branches going to the Mm. mylohyoidei posterior as profundus and superficialis.

The second branch, the ramus muscularis et glandularis, also arises from the portio alveolaris inferior of the mandibular ramus. A branch extends to the Mm. mentalis superficialis, mentalis profundus anterior, and mentalis profundus posterior. It also enters the portiones major and minor of the M. genioglossus.

A third branch, the ramus lingualis, originates from the ramus mandibularis before the latter enters the alveolar canal. This branch emerges from the canal to pass along the ventral buccal floor, where it joins the ramus lingualis anterior of the hypoglossal nerve. It enters the lingual sheath and then the tongue, extending to the anteriormost extremity of the terminal prongs to innervate, with the hypoglossal nerve, the bundles of the M. hyoglossus.

2. *N. facialis*: The facial nerve emerges from the cranium and divides into an anterior branch, the ramus palatinus, and a posterior branch, the ramus hyomandibularis. The latter branch extends posteriorly as the ramus hyoideus to innervate the Mm. geniolateralis and constrictor colli.

3. *N. hypoglossus*: The hypoglossal nerve extends obliquely posterior along the dorsal side of the neck to the buccal floor, where it divides into two branches, each of which further subdivide into two branches. One branch forms the rami ad musculum geniotrachealis, and the second branch gives rise to the rami linguales anterior and posterior.

The ramus ad musculum geniohyoideum extends obliquely over the M. ceratohyoideus to form two branches that innervate the middorsal region of the M. geniohyoideus and lateral surface of the M. constrictor colli, respectively.

The ramus ad musculum ceratohyoideum et musculum mandibulotrachealis extends from the M. interportalis to the M. ceratohyoideus, innervating these and also sending branches to the Mm. cornuohyoideus and mandibulotrachealis.

The third branch (ramus lingualis anterior) originates from the hypoglossal nerve and extends along the lateral border of the tongue to eventually anastomose with the ramus lingualis of the mandibular ramus of the trigeminal nerve. As it does so, it sends branches to the sublingual glands and terminates in the M. genioglossus. A small branch also extends to both the Mm. genioceratoideus and mandibuloproximalis.

The ramus ad musculum mandibulohyoideum is derived from the hypoglossal nerve before the branching of the ramus lingualis posterior. It innervates the M. mandibulohyoideus.

Two other branches derived from the hypoglossal (lingual accessorii) innervate the posterior part of the base of the tongue. A final branch, the ramus lingualis posterior, is the terminal portion of the hypoglossal nerve. It also innervates the basal area of the tongue.

Some information is available for other lizards such as *Chamaeleo* and *Calotes* (Gnanamuthu 1937), in which the formation of the lingual nerve varies. The lingual branch of the hypoglossal in *Chamaeleo* is separated from the glossohyoidean plexus and forms two branches, the rami linguale lateralis and medialis. The ramus lingualis lateralis extends posteriorly to innervate the M. genioglossus, and the main branch anastomoses with the lingual branch of the Vth cranial nerve; together they penetrate the M. hyoglossus and join the ramus lingualis medialis that enters and innervates the M. hyoglossus. This same branch in the anterior region of the buccal floor unites with the combined lingual branch and with it also enters the tongue. In

Calotes the lingual branch of the hyoglossal nerve extends one branch to the M. genioglossus and one to the tongue. The main branch unites with a ramus of the trigeminal to penetrate the tongue and there subdivides into many branches for innervation of the tongue muscles.

Sondhi (1958) gives the following nerve pattern for the buccal floor of *Natrix* (*Xenochrophis*), a natricid snake:

1. *N. trigeminus*: The ramus mandibularis of the trigeminal nerve sends three branches to the buccal floor. The first branch (ramus ad musculum mylohyoideum) originates from the mandibular ramus immediately after the latter enters the alveolar canal of the dentary as the portio alveolaris inferior. It divides into two branches, one innervating the M. mylohyoideus posterior profundus and the other the M. mylohyoideus posterior.

A second branch, the ramus muscularis et glandularis, originates from the portio alveolaris inferior of the mandibular ramus. After emerging from the mandible, it extends medially to provide branches for the Mm. intermaxillaris, genioglossus portio major, mentalis profundus anterior, and mentalis profundus posterior.

The third branch (ramus lingualis) arises from the portio alveolaris inferior of the mandibular ramus after the mandibularis et glandularis. It unites with the ramus lingualis of the hyoglossal nerve and extends medially to the lingual sheath and M. hyoglossus.

2. *N. facialis*: The facial nerve emerges from the foramen prooticum and extends to the M. mylohyoideus posterior as the ramus hyomandibularis, which has two branches to that muscle.

3. *N. hypoglossal*: The hypoglossal nerve has three main branches, including the ramus descendens that originates as a thin branch extending posteriomedially to innervate the ventral surface of the Mm. omohyoideus, sternohyoideus, and sternothyroideus.

The second branch is the main stem of the hypoglossal nerve, which forms the ramus lingualis posterior. It extends forward as two branches, one entering the body and the other the base of the tongue.

The third branch, the ramus ad musculum geniolateralis, originates in the hypoglossal nerve almost opposite the ramus lingualis posterior and innervates the M. geniolateralis. Distally the hypoglossal bifurcates into two branches, an inner ramus ad musculum mandibulotrachealis and an outer ramus ad musculum geniohyoideum. The inner division extends anteriorly and medially to innervate the posterior part of the M. mandibulotrachealis. The outer branch extends anterolaterally to form two branches that innervate the M. geniohyoideus.

Langebartel (1968) has summarized the innervation of the muscles of the buccal floor in other snakes. The mandibular division of the trigeminal nerve innervates the M. intermandibularis and parts of the tongue. The facial innervates part of the Mm. constrictor colli and the cervicomandibularis and sends some branches to the tongue. Some branches from glossopharyngeal and the vagus innervate the M. ceratomandibularis, but only one branch innervates the M. hyotrachealis. The hypoglossal nerve innervates the Mm. geniohyoideus, ceratomandibularis, and sternohyoideus. The Mm. genioglossus and hypoglossus are innervated by an anterior branch of the hypoglossal nerve. Very commonly the glossopharyngeal, vagus, and hypoglossal nerves combine to innervate the lingual sheath and the Mm. genioglossus and hypoglossus. The hypoglossal may also have anterior and posterior branches that enter the tongue. Last, an anterior branch of the hypoglossal unites with a branch of the trigeminal to innervate the Mm. genioglossus and geniotrachealis. Varkey (1979) describes the innervation of muscles in *Nerodia*, but does not attempt to identify the nerves.

Soliman (1964) describes and figures the cranial nerves of *Chelydra serpentina*. Colored plates depict the various nerves entering the muscles associated with the buccal floor and the tongue.

Trionyx has been described by Sondhi (1958), who indicates the existence of the following nerve pattern, comparable to that reported for *Chelydra*:

1. *N. trigeminus*: The mandibular ramus of the trigeminal nerve has two branches, including the ramus ad musculum mylohyoideum that arises in *Varanus* and *Natrix*, and the ramus lingualis. The former branch extends posteriorly along the medial side of the mandible to divide into two branches, one of

which innervates the M. mylohyoideus anterior and the other which innervates the M. mylohyoideus posterior. The ramus lingualis arises from the portio alveolaris inferior and emerges from the mandible through a small foramen to innervate the M. genioglossus. Soliman and Hegazy (1971) also describe this nerve in *Chalcides ocellatus*.

2. *N. facialis*: The facial gives rise to the ramus hyomandibularis, which innervates the buccal floor. It extends posteriorly as the ramus digastricus and sends a branch to the M. constrictor colli and another to the M. constrictor superficialis.

3. *N. hypoglossus*: The hypoglossal nerve extends along the anterior part of the neck to the M. ceratohyoideus, where it gives rise to two branches, the rami descendens and ad musculum sternothyroideum. A third branch (ramus ad musculum geniohyoideum) is formed as it emerges on the ventral side of the M. ceratohyoideus. Finally, it extends anteriorly to provide the ramus lingualis and then terminates by dividing into two branches, the rami ad musculum entoglossohypoglossalis and ad musculum hypoglossolateralis.

The ramus descendens extends anteromedially beyond the second ceratobranchial to form two branches that innervate, respectively, the Mm. omohyoideus and the sternohyoideus. The ramus ad musculum sternothryoideum extends across the surface of the Mm. omohyoideus and sternohyoideus to innervate the M. sternothyroideus. The ramus ad musculum ceratohyoideus extends to the dorsal surface of the M. ceratohyoideus, which it innervates. The ramus ad musculum mandibulohyoideum is a small branch extending anteriorly to innervate the ventral surface of the M. mandibulohyoideus. The ramus ad musculum geniohyoideum extends anteriorly to form two branches, with one innervating the portio ventralis and the other entering the portio distalis of the M. geniohyoideus. The ramus lingualis extends medially to enter the base of the tongue, where it passes anteriorly inside the tongue to innervate the M. hyoglossus. As in *Lissemys*, there are no anastomoses with the lingual branch of the trigeminal. The ramus ad musculum entoglossohypoglossalis is a delicate branch innervating the M. entoglossohypoglossalis. Finally, the ramus ad musculum hypoglossolateralis extends obliquely lateral to innervate the M. hypoglossolateralis.

Sondhi (1958) has investigated the nerve patterns of the buccal floor seen in *Gavialis* and presents the following pattern.

1. *N. trigeminus*: The mandibular ramus of the trigeminal nerve forms two branches, the rami ad musculum mylohyoideum and lingualis. The former emerges from the dentary and passes posteriorly to innervate the dorsal surface of the M. constrictor colli. The ramus lingualis emerges from a foramen after arising from the portio alveolaris inferior. It passes obliquely anterior to innervate the M. genioglossus portio major.

2. *N. facialis*: The ramus hyomandibularis of the facial nerve sends a branch, the ramus hyoideus digastricus, of Sondhi, posterior to the neck to divide into two branches. The first branch innervates the M. constrictor pharyngis and the second extends dorsally to the Mm. constrictor colli and constrictor superficialis.

3. *N. hypoglossus*: On the dorsal side of the neck the hypoglossal nerve divides into four branches. The first branch, or ramus descendens, divides into two branches at or near the middle of the M. omohyoideus. These branches innervate the M. omohyoideus and the M. sternohyoideus, respectively. The second branch, ramus ad musculum sternohyoideum, passes obliquely posterior to divide into several branches that innervate the M. sternohyoideus. The ramus lingualis posterior forms the third branch and sends a subdivision, the ramus ad musculum geniohyoideum, to the M. geniohyoideus, and other branches enter the tongue and innervate the M. geniohyoideus portio major. The last branch, ramus lingualis anterior, extends posteriorly to the mandible to innervate the Mm. ceratohyoideus and mandibulohyoideus, and other branches extend anteriorly to enter the tongue and the Mm. genioglossi portiones minor and major.

Reese (1915) indicates that the ramus mandibularis (ramus maxillaris inferior of Reese) of the crocodile divides into two and then four branches. Two of these branches in nervate the M. mylohyoideus. The M. hyoglossus is served by branches of the IXth and XIIth nerves. The hypoglossal nerve also sends branches to the Mm. omohyoideus, sternohyoideus, geniohyoideus and ge-nioglossus.

B. Spinal Nerves

Oelrich (1956) reports that in *Ctenosaura* the first spinal nerve innervates the ventral part of the M. omohyoideus and the dorsal part of the sternohyoideus. Sondhi (1958) indicates that in *Varanus* and *Natrix* the united stems of the first and second spinal nerves anastomose with the hypoglossal nerve and extend posteriorly in the neck to send small branches to the Mm. sternohyoideus and sternothyroideus and a large branch to the M. omohyoideus. Some of the succeeding spinal nerves also innervate the M. constrictor colli.

In *Natrix,* as in *Varanus,* the first and second spinal nerves innervate parts of the M. constrictor colli. In some other snakes many spinal nerves innervate the Mm. neuromandibularis, costomandibularis, costo-cutanei inferior and superior, omohyoideus, sternohyoideus, and transverus branchialis.

In *Trionyx, Gavialis,* and *Crocodylus* the united stem of the first and second spinal nerves innervates the M. constrictor colli, whereas in *Crocodylus* numerous branches of first, second, and third spinal nerves innervate the smaller ventral muscles of the neck.

IX. DISCUSSION

An examination of the preceding descriptions show that the information on the hyoid and associated structures was widely scattered and incomplete. Although morphology is one of the oldest branches of biology, there is an absence of complete accounts of the gross anatomy of the buccal floor of reptiles as a class. Similar gaps in our knowledge exist for other anatomical areas of the reptilian body. In spite of our acceptance of some reptilian ancestral stocks as being the lines of descent for birds and mammals, anatomists have not vigorously pursued studies to show phylogenetic relationships. The lack of a complete understanding of these groups is astounding considering the important phylogenetic position of reptiles.

Despite the lack of information, some generalizations can be made. As indicated by Sondhi (1958), the buccal floor in many reptiles has three functions: (1) it participates in the act of inspiration and expiration, (2) it aids in the capture and the deglutition of food, and (3) it provides the mechanisms of tongue movement. To Sondhi's list should be added two additional functions: (4) behavioral display and (5) sensory reception.

The important role of the buccal area as a respiratory throat pump has been explored by Gnanamuthu (1937), who demonstrated the part played in *Hemidactylus.* He states,

> The contraction of the thorax expelling air would result in the inflation of the buccal cavity, and when next the thorax relaxes this impure air may be taken into the lungs again, because the thoracic contraction and expansion follows each other so rapidly. However, the elevation of the mouth floor and tongue through the aid of transverse and hyoid muscles just when the thorax contracts serves to expel the vitiated air effectively out of the body.

Respiratory mechanisms in reptiles vary widely. *Calotes* utilizes the limbs of the anterior cornua and the attached muscles to actively raise and lower the throat. The positions of cornua and ceratobranchials and associated muscles in *Varanus* indicate a change of the volume of the throat caused by dilation and compression of the floor of the mouth.

Among the testudines, the posterior part of the M. hyoglossus and the entire Mm. ceratohyoideus, entoglossohypoglossalis, and hypoglossolateralis utilize the jointed basihyoid and hypoglossum to move the throat up and down as one solid piece. Although these structures may not be important in respiration (Mitchell and Morehouse 1863), there is reason to believe that both aquatic and terrestrial turtles pump the throat to exchange water and air in the nasal canals and buccal cavity for sensory functions (McCutcheon 1943). In Figure 19 we attempt to reproduce the extensive fimbriations on the buccopharyngeal floor of *Trionyx.* The total function of these numerous filaments may not be fully understood, but seemingly they are important in aquatic respiration (Girgis 1961).

In snakes, inspiration and expiration are accomplished by the muscles of the body wall compressing the lungs for expiration and expanding for inspiration. A minor contribution is made by the expansion and contraction of the anterior part of the body. As a result, the hyoid has become greatly reduced and contributes mostly as a support for the buccal floor and as a support for the muscles and membranes that open and close the glottis. For further information on respiration in vertebrates, see Hughes (1963), Gans and Hughes (1967), Bishop and Foxon (1968), and Gans (1969).

Food capture and deglutition in reptiles is difficult to correlate with the morphology of the buccal floor. For example, snakes have a ligamentous connection between the mandibular rami and movable articulations of the maxilla, palatine, pterygoid, and quadrate, which allow for the movement of one side of the jaw apparatus to move forward and secure a firm hold on the prey before moving the other side, as indicated by Gans (1961) and Frazzetta (1966). Such a situation does not exist in the Lacertilia, Amphisbaenia, Rhychocephalia, Testudines, or Crocodylia, making comparisons difficult, if not impossible. In the latter three groups, however, the food capturing and swallowing mechanisms are basically similar owing to the greater similarity of throat anatomy.

The movement of the tongue is important in most reptiles because of its sensory nature and association with Jacobson's organ. The tongue is simplest in the primitive testudines and Crocodilia, indicating a more ancient and conservative nature in these groups. The primitive lizards, such as iguanids, and some testudines, such as *Gopherus*, have a thick, fleshy tongue, used both for sensory activities and manipulation of the food within the mouth (Avery and Tanner, 1971; Gnanamuthu, 1937). An advanced lizards, such as *Varanus*, the tongue is similar to that of snakes in gross morphology. The fact that the associated throat musculature in these two groups differs is an indication that perhaps the manipulation of the tongue in varanids and snakes has been, at least partially if not completely, freed from the buccal floor musculature.

Last, the buccal floor has behavioral implications in many lizards, particularly the iguanids, in which males often have enlarged throat dewlaps. The behavioral implications of these structures is beyond the scope of this paper [see work of Carpenter 1965 (*Anolis*), 1967, 1977 (Iguanids), 1970 (Agamids)], but in the forms with the best developed dewlaps, such as *Anolis* and *Iguana*, the second ceratobranchials and associated musculature provide the main structural components of movement.

Some generalizations about the buccal floor can also be made. The more primitive the organism, the less complicated and specialized the gross anatomy of the buccal floor. This is apparently true for most orders, although there are exceptions within some orders (such as in some testudines). In the primitive forms, the hyoid has retained more cornua, some specialized muscles are absent, and the tongue is less differentiated. In the more advanced forms, such as lizards, the hyoid has become complex and the musculature has proliferated and specialized.

Lizards show a greater variation in the morphology and function of the tongue than do other groups of reptiles. Tongues are structured for food manipulation (Iguanidae and Amphisbaenia), food getting (Chamaeleonidae and Amphisbaenia), and also for sensory functions in such groups as *Cnemidophorus*, *Heloderma*, and *Varanus*. Such functional variations have in turn altered the basic morphology of the buccal floor to accommodate the adaptive feeding habits and the associated sensory and behavioral activities. In snakes specializations of feeding and life habits have caused a secondary reduction of many elements of the buccal floor, particularly in the skeletal structures, and the tongue is no longer a manipulator of food. In snakes the tongue is filamentous and important primarily as a sense organ. As indicated by Sondhi (1958), there is a structural similarity between the tongues of some lizards (*Varanus*) and snakes. This, Sondhi reasoned, may have led to the development of the highly sensitive tongues of snakes. At least, such lizards have a flexible tongue and the terminal forking is structurally similar enough to suggest an evolutionary relationship. Perhaps this is an example of convergence of structure to perform a similar function in distantly related groups.

In general it is difficult to draw major phylogenetic conclusions from the buccal floor because the scope of such a study is necessarily limited to one specialized area and can be misleading. When hyoid elements are lost, the associated muscles are also lost or may become unrecognizable. Thus the implication of presence or absence of structures is also misleading. Future morphological phylogenetic studies in the area of the buccal floor should be supplemented by embryological information, as indicated by DeBeer (1930, 1951) and Edgeworth (1935). Such research will provide clues as to which structures have been lost, fused, readapted or never possessed by an organism.

Acknowledgments

We wish to thank those who have aided us during the preparation of this study, particularly our own institutions who have provided space and secretarial help and have permitted us to dissect materials from their collections (Brigham Young University Life Science Museum, BYU, and Southern Connecticut State College, SCSC). We have also received study materials from the following: Dr. George R. Zug, U.S. National Museum; Dr. Carl Gans, University of Michigan; Dr. Alan E. Leviton, California Academy of Sciences; Dr. Richard G. Zweifel, American Museum of Natural History, and Mr. Jose P. Rosado, Museum of Comparative Zoology. We received, on exchange, specimens from Dr. F. H. Rehmani, Zoologische Museum, Kanpur, India. These were very helpful as comparative materials, and for their use we are indeed grateful.

We have used freely skeletal and dissected material used in previous studies at our laboratories. These have served us not only as source materials, but also for the comparative studies.

We are grateful to Dr. Robert M. Winokur, who read the manuscript and provided helpful suggestions in those areas where Chelonians are discussed.

In the preparation of this study we have relied heavily on the studies of Gnanamuthu (1937), Langebartel (1968), and Sondhi (1958). Because these are basic studies dealing in some detail with the buccal area, we refer to them repeatedly. Without them this study would have been extremely difficult.

Bibliography and Literature Cited

Adams, L. A. 1919. A memoir on the phylogeny of the jaw muscles in recent and fossil vertebrates. Ann. N.Y. Acad. Sci. 28:51–166.

_____. 1925. Correlations of the musculature and the movements of the skull in *Natrix*, with some suggestions of homology in the lacertilian. Morph. 41:159–181.

Albright, R. G., and E. N. Nelson. 1959. Cranial kinetics of the generalized colubrid snake *Elaphe obsoleta quadrivittata*, I and II. J. Morph. 105:193–192.

Anthony, J., and R. G. Serra. 1949. Sur une particularite remarguable del'appareil de la morsure chez un serpent Aglyphe de l'Amerique tropicale, *Xenodon merremii*. Rev. Brasil. Biol. 9(2):153–160.

_____. 1950. Anatomie de l'appareil de la morsure chez *Eunectes murinus*. Rev. Brasil. Biol. 10(1):23–24.

Ashley, L. M. 1955. Laboratory anatomy of the turtle. Wm. C. Brown Company Publishers, Dubuque, 49 pp.

Avery, D. F., and W. W. Tanner. 1964. The osteology and myology of the head and thorax regions of the *obesus* group of the genus *Sauromalus* Dumeril (Iguanidae). BYU Sci. Bull., Biol. Ser. 5(3):1–30.

_____. 1971. Evolution of the iguanine lizards (Sauria, Iguanidae) as determined by osteological and myological characters. BYU Sci. Bull., Biol. Ser. 12(3):1–79.

Auen, E. L., and D. A. Langebartel. 1977. The cranial nerves of the colubrid snakes *Elaphe* and *Thamnophis*. J. Morph. 154(2):205–222.

Barrows, S., and H. M. Smith. 1947. The skeleton of the lizard *Xenosaurus grandis* (gray). Univ. Kansas Sci. Bull. 31(2,12):227–275.

Beddard, F. E. 1905a. Some notes on the cranial osteology of the Mastigure lizard—*Uromastix*. Proc. Zool. Soc. London 1905:1–9.

_____. 1905b. A contribution to the anatomy of the frilled lizard (*Chlamydosaurus kingi*) and some other Agamidae. Proc. Zool. Soc. London 1905:9–22.

_____. 1907. Contributions to the knowledge of the systematic arrangement and anatomy of certain genera and species of Squamata. Proc. Zool. Soc., London 1907:35–59.

Bellairs, A. d'A. 1950. Observations on the cranial anatomy of *Anniella* and a comparison with that of other burrowing lizards. Proc. Zool. Soc. London. 119:887–904.

Bergman, R. A. M. 1961. The anatomy of some Viperidae. Acta Morph. Neerl-Scand 4(3):195–230.

_____. 1965. The anatomy of *Calamaria multipunctata* (Boie). Bull. Nat. Mus. Singapore 33(7):35–66.

Bishop, I. R., and G. E. H. Foxon. 1968. The mechanism of breathing in the South American lungfish, *Lepidosiren paradox*: a radiological study. J. Zool. London. 154:263–271.

Bissinger, B. E., and C. A. Simon. 1979. Comparison of tongue extrusions in representatives of six families of lizards. J. Herpetology 13(2):113–139.

Bogert, C. M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Amer. Mus. of Nat. Hist., Vol. 105(1).

Bojanus, L. H. 1819. Anatome testudinis europaeae. 1970 ed. Society for the Study of Amphibians and Reptiles. Vol. VI, 179 pp.

Boltt, R. E., and R. F. Ewer. 1964. The functional anatomy of the head of the puff adder, *Bitis arietans* (Merr). J. Morph. 114:38–106.

Bradley, O. C. 1903. The muscles of mastication and the movements of the skull in Lacertilia. Zool. Fb., Abt. Anat. 18:475–488.

Branch, W. R. 1982. Hemipeneal morphology of the platynotan lizards. J. Herpetology, 16(1):16–38.

Brock, G. T. 1938. The cranial muscles of the gecko, a general account with a comparison of the muscles in other Gnathostomes. Proc. Zool. Soc. London, Series B. 180,761.

Bullock, R. E., and W. W. Tanner. 1966. A comparative osteological study of two species of Colubridae (*Pituophis* and *Thamnophis*). BYU Sci. Bull., Biol. Ser. 8(3):1–29.

Byerly, T. G. 1926. The myology of *Sphenodon*. Univ. Iowa Study Nat. Hist. 11.

Camp, C. L. 1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist. 48(11):289–481.

Carpenter, C. C. 1965. The display of the Cocos Island Anole. Herpetologica 21(4):256–260.

______. 1967. Aggression and social structure in Iguanid lizards. Univ. of Missouri Press, Columbia.

______. 1977. The aggressive displays of three species of South American iguanid lizards of the genus *Tropidurus*. Herpetologica 33(3).

Carpenter, C. C., J. A. Badham, and B. Kimble. 1970. Behavior patterns of three species of *Amphibolurus* (Agamidae). Copeia (3)497–505.

Chaine, J. 1902. Considerations sur la constitution musculaire de la region sus-hyoidienne chez les vertebres en general. Ann. Sci. Natur. 16:375–393.

Chiasson, R. B. 1962. Laboratory anatomy of the alligator. Wm. C. Brown Company Publishers, Dubuque, 56 pp.

Cope, E. D. 1892. The osteology of the Lacertilia. Proc. Amer. Philos. Soc. 30(138):185–221.

______. 1898(1900). Crocodiles, lizards, and snakes of North America. Ann. Rept. U.S. Nat. Mus., pp. 953–954.

Cox, D. C., and W. W. Tanner. 1977. Osteology and myology of the head and neck regions of *Callisaurus, Cophosaurus, Holbrookia*, and *Uma* (Reptilia: Iguanidae). Great Basin Nat. 37(1):35–56.

Cowan, I. M., and W. B. M. Hick. 1951. A comparative study of the myology of the head region in three species of *Thamnophis* (Reptilia, Ophibia). Trans. Roy. Soc. Canada 45:19–60.

Criley, B. B. 1968. The cranial osteology of gerrhonotiform lizards. Amer. Midl. Nat. 80(1):199–219.

Cundall, D. L. 1974. The cranial osteology amd myology of the green snakes, genus *Opheodrys*. Diss. Abstr. Int. B. Sci. Eng. 35(6):3109–3110.

Davis, D. D. 1934. The collared lizard, a laboratory guide. Macmillan, New York, 57 pp.

DeBeer, G. R. 1930. Embryology and evolution. Clarendon Press, Oxford.

______. 1937. The development of the vertebrate skull. Clarendon Press, Oxford.

______. 1951. Embryos and ancestors. Clarendon Press, Oxford.

DeVis, C. W. 1883. Morphology of *Chlamydosaurus kingi*. Proc. Linn. Soc. New South Wales. 1883:1–320.

Duda, W. 1965. On the cranial osteology of *Agama tuberculata* with a note on the comparative study of the skulls in the family Agamidae. Vestn. Ceshosl. Zool. Spalc. 29:156–174.

Dullemeijer, P. 1956. The functional morphology of the head of the common viper, *Vipera berus* (Linn.) Arch. Neerl. Zool. 12:387–497.

______. 1959. A comparative functional-anatomical study of the heads of some Viperidae. Morph. Jahrb. 99:881–985.

Edgeworth, F. H. 1931. On the development of the external ocular masticatory and hyoid muscles of *Sphenodon punctatus*. Proc. Zool. Soc. London. 1931:803–808, 817–818.

______. The cranial muscles of vertebrates. Univ. of Cambridge Press. Cambridge, England, 494 pp.

El Toubi, M. R. 1938. The osteology of the lizard *Scincus scincus* (Linn.) Bull. Fac. Sci. Cairo. Fouad I Univ. 14(1938):5–38.

______. 1947a. Some observations on the osteology of the lizard *Agama stellio* (Linn.). J. Morph. 81:135–149.

______. 1947b. Notes on the cranial osteology of *Uromastix aegyptia* (Forskal). Bull. Fac. Sci. Fouad I Univ. 25(1947):1–3.

El Toubi, M. R., and A. M. Kamal. 1952. The cranial osteology of Egyptian Geckos. Bull. de l'institut Fouad Ier du Desert. 11(1947):1–3.

______. 1959a. The development of the skull in *Chalcides ocellatus*. J. Morph. 105:55–104.

______. 1959b. The development of the skull of *Chalcides ocellatus*. I. The development of the chondrocranium. J. Morph. 104:269–306.

El Toubi, M. R., and I. M. A. Majid. 1961. A comparative study of the cranial osteology of the Egyptian vipers. J. Arib. Vet. Med. Assoc. 21:303–325.

Eyal-Giladi, H. 1964. The development of the chondrocranium of *Agama stellio*. Acta Zool. Stockh. 45:139–165.

Evans, H. E. 1955. The osteology of a worm snake, *Typhlops jamaicensis* (Shaw). Anat. Rec. 122(3):381–396.

Fanghella, C., D. F. Avery, and W. W. Tanner. 1975. *Urosaurus* and its phylogenetic relationship to *Uta* as determined by osteology and myology (Reptilia: Iguanidae). Great Basin Nat. 35:245–268.

Fisher, D. L., and W. W. Tanner. 1970. Osteological and myological comparisons of the head and thorax regions of *Cnemidophorus tigris septentrionalis* Burger and *Ameiva undulata parva* Barbour and Noble (Family Teiidae). BYU Sci. Bull., Biol. Ser. 11(1):1–41.

Frank, G. H., and A. L. Smit. 1974. The early ontogeny of the Columella auris of *Crocodilus niloticus* and its bearing on problems concerning the upper end of the reptilian hyoid arch. Zool. Africana 9:59–88.

Frazzetta, T. 1966. Studies on the morphology and function of the skull in the Boidae (Serpentes), Part II. Morphology and function of the jaw apparatus in *Python sebae* and *Python molurus*. J. Morph. 118:217–296.

Furbringer, M. 1922. Das Zungenbein der Wirbeltiere. Abhandl. Heidenberger Akad. Wiss. Nath-naturwiss., Kl. B., Abh. 11:1–164.

Gandolfi, H. 1908. Die zunge der Agamidae und Iguanidae. Zool. Anz. 32:569–580.

Gans, C. 1961. The feeding mechanisms of snakes and its possible evolution. Ameri. Zool. 1:217–227.

———. 1969. Bullfrog (*Rana catesbeiana*) ventilation: how does the frog breathe? Science 1963: 1223–1225.

Gans, C., and G. M. Hughes. 1967. The mechanism of lung ventilation in the tortoise *Testudo gracca* Linne. J. Exp. Biol. 47:1–20.

Gasc, J. P. 1968. Contribution a l'osteologie et a la myologie de *Dibamus novaeguineae* Gray (Sauria, Reptilia), discussion systematique. Ann. Sci. Nat. Zool. Biol. Anim. 10:127–150.

George, J. C. 1948. The muscular system of *Uromastix hardwickii* (Gray). J. Univ. Bombay. 17(3):1–17.

———. 1954. On the cranial osteology of *Uromastix*. J. Anim. Morph. and Phys. 1(2):23–29.

George, J. C., and R. V. Shad. 1954. The myology of the head and neck of the Indian pond turtle, *Lissemys punctata granoso* (Schoepff). J. Anim. Morph. Physiol. 1:1–12.

———. 1955. The myology of the head and neck of the Indian tortoise, *Testudo elegans*. J. Anim. Morph. Physiol. 2:1–13.

Gibson, F. W. 1966. Head muscles of *Boa constrictor*. Zoologica 51:29–48.

Girgis, S. 1961. Contribution a l'osteologie et a la myologie de *Dibamus novaeguineae* Gray (Sauria, Reptilia), discussion systematique. Comp. Biochem. Physiol. 3:206–217.

Gnanamuthu, C. P. 1930. The anatomy and mechanism of the tongue of *Chamaeleon carcaratus* (Merrem). Proc. Zool. Soc. London. Part II, 467–486.

———. 1937. Comparative study of the hyoid and tongue of some typical genera of reptiles. Proc. Zool. Soc. London, Ser. B. 107:1–63.

Goppert, E. 1900. Der Kehlkopr der Amphibien und Reptilien. Morph. Jahrb. 28:1–27.

———. 1903. Bedeutung der Zunge für den Sekundaren Gaumen und Ductus Naso-pharyngeus. Morph. Jahrb. 31:311–357.

Gräper, L. 1932. Die das zungenbein und zunge bewegenden muskeln der Schildkroten I. Jena Zschr. Natura, 66:169–198.

Haas, G. 1930. Über die kaumuskulatur und die schädelmenchanik einiger wuhlschlangen. Zool. Jahrb. Anat. Jena. 52:95–218.

———. 1981. Die kiefermuskulatur und die schädelmenchanik der schlangen in vergleichender darstellung. Zool. Jahrb. Anat. Jena. 53:127–198.

———. 1931b. Über die morphologie der kiefermuskulatur und die schädelmechanik einiger schlangen. Zool. Jahrb. Anat. Jena. 54:333–416.

———. 1952. The head muscles of the genus *Causus* (Ophidia, Solenoglypha) and some remarks on the origin of the Solenoglypha. Proc. Zool. Soc. London. 122:573–592.

———. 1960. On the trigeminus muscles of the lizards *Xenosaurus grandis* and *Shinisaurus crocodilurus*. Amer. Mus. Novitates 2017:1–54.

———. 1968. Anatomical observations on the head of *Anomalepis aspinosus* (Typhlopidae, Ophibia). Acta Zoologica 49:63–139.

———. 1973. Muscles of the jaws and associated structures in the *Rhynchocephalia* and Squamata. Biology of the reptilia, Vol. 4 Academic Press, London and New York. 285–490.

Hacker, G., and G. H. Schumacker. 1955. Die muskeln und fascien des mundbodens bei *Testudo graeca*. Anat. Ang. 101:294–305.

Harris, V. A. 1963. The anatomy of the rainbow lizard, *Agama agama*. Hutchison Tropical Monographs. Anchor Press, 104 pp.

Hershkowitz, J. 1941. On the finer structure of the tongue of *Lichanura roseofusca*. J. Morph. 68(1):71–79.

Heymans, J. C. 1970. Sur le complexe musculaire de l'appareil de morsure de natriciteres (Colubridae). Natur. Belg. 51(7):323–332.

———. 1975. La musculature mandibulaire et le groupe parotidien des aparallactinae and atractaspinae. Rev. Zool. Afr. 89(4):889–905.

Howes, G. B., and H. H. Swinnerton. 1901. On the development of the skeleton of the tuatara, *Sphenodon punctatus*, with remarks on the young, on the hatching, and on the hatching hour. Trans. Zool. Soc. London. 16:1–86.

Hughes, G. M. 1963. Comparative physiology of respiration. Harvard Univ. Press. Cambridge, Massachusetts.

Iordansky, N. N. 1970. Structure and biomechanical analysis of functions of the jaw muscles in the lizards. Anat. Anz. 127(4),383–413.

Islam, A. 1955. The skull of *Uromastix hardwickii* (Gray). Biologica Lahore. 1(2):141–196.

Islam, A., and S. Ashig. 1972. The cranial nerves of *Uromastix hardwicki* Gary. Biologica (Lahore) 18(1):51–73.

Iyer, M. M. N. 1942. The habits, external features, and skeleton system of *Calotes versicolor*. Part 1. J. Mysore Univ., Sec. B. 3(1942):153–170.

———. 1943. The habits, external features and skeletal system of *Calotes versicolor* (Daud). Part II. The Skull. J. Mysore Univ., Sec. B. 4(1943):115–151.

Jenkins, R. L., and W. W. Tanner. 1968. Osteology and Myology of *Phrynosoma p. platyrhinus* Girard and *Phrynosoma p. hernandesi* Girard. BYU Sci. Bull., Biol. Ser. 9(4):1–34.

Johnson, C. E. 1922. Branchial derivatives in turtles. J. Morph. 36:299–329.

Jollie, M. J. 1960. The head skeleton of the lizard. Acta Zool. Stockh. 41:1–64.

Kallius, E. 1901. Beitrage zur Entwicklung der Zunge. I. Teil Amphibian und Reptilien. Anat. Hefte 16:529–760.

Kamal, A. M., and H. G. Hammouda. 1965. The development of the skull of *Psammophis sibilans*. J. Morph. 116:197–296.

Kamal, A. M., H. G. Hammouda, and F. M. Mokhtar. 1970. The development of the osteocranium of the Egyptian cobra. III. The otic capsule, palate, temporal bones, lower jaw, and hyoid apparatus of the osteocranium. Acta Zool. (Stockholm) 51(1–2):31–42.

Kardong, K. V. 1973. Lateral jaw and throat musculature of the cottonmouth snake *Agkistrodon piscivorus.* Gegenbaurs Morph. Jahrb. Leipzig 119(3):316–335.

______. 1974. Kinesis of the jaw apparatus during the strike in the cottonmouth snake *Agkistrodon piscivorus.* Forma et Functio. 7(4):327–354.

______. 1977. Kinesis of the jaw apparatus during swallowing in the cottonmouth snake *Agkistrodon piscivorus.* Copeia 1977(2):338–348.

Kesteven, J. L. 1944. The evolution of the skull and the cephalic muscles. A comparative study of their development and adult morphology. Memoir Australian Mus., Sydney 8(3):237–264.

Kingman, R. H. 1932. A comparative study of the skull in the genus *Eumeces* of the family Scincidae. Bull. Univ. Kansas. 33(1932):273–295.

Kluge, A. 1962. The comparative osteology of the eublepharid lizard genus *Coleonyx* Gray. J. Morph. 110:299–332.

Kochva, E. T. 1958a. The head muscles of *Vipera palaestinae* and their relation to the venom gland. J. Morph. 102:23–54.

______. 1958b. On the lateral jaw musculature of the solenoglypha with remarks on some other snakes. J. Morph. 110:227–284.

Kroll, J. C. 1973. Taste buds in the oral epithelium of the blind snake, *Leptotyphops dulcis* (Reptilia Leptotyphopidae). Southwestern Nat. 17:365–370.

Langebartel, D. A. 1968. The hyoid and its associated muscles in snakes. Illinois Biological Monograph No. 38. Univ. of Illinois Press, Urbana.

Lakjer, T. 1927. Studien über die Gaumenregion bei Sauriern im Vergleich mit Anamniern und Sauropsiden. Zool. Fb., Abt. Anat. 49:57–356.

Lasana, M. 1834. Essai sur l'os hyoido de quelques reptiles. Memoire della r. Accademia della Science de Torino. 37:1–25.

Liem, K. F., H. Marx, and G. B. Rabb. 1971. The viperid snake *Azemiops*: its comparative cephalic anatomy and phylogenetic position in relation to Viperinae and Crotalinae. Fieldiana Zool. 59(2):67–126.

Lightoller, G. H. S. 1939. Probable homologues. A study of the comparative anatomy of the mandibular and hyoid arches and their musculature. Part I. Comparative myology. Trans. Zool. Soc. London 24:349–444.

List, J. C. 1966. Comparative osteology of the snake families Typhlopidae and Leptotyphlopidae. Illinois Biological Monographs. No. 36. Univ. of Illinois Press, 112 pp.

Lubosch, W. 1932. Bemerkungen über die zungenmuskulatur de Chamaleons. Morph. Jahrb. 71:158–170.

______. 1933. Untersuchungen über die visceralmusculatur der sauropiden. Morph. Jahrb. 72:584–666.

Mahendra, B. C. 1947. Contributions to the bionomics, anatomy, reproduction, and development of the Indian house gecko, *Hemidactylus flaviviridis* Ruppel. Part IV. The respiration and vocal organs. Proc. Ind. Acad. Sci. 25:57–73.

______. 1949. The skull of the Indian house gecko *Hemidactylus flaviviridus* Ruppel. Proc. Zool. Soc. Calcutta. 2(1949):29–42.

Malam, M. E. 1941. Cranial anatomy of the genus *Gerrhosaurus.* South African J. Sci. 37:192–217.

McCutcheon, F. H. 1943. The respiratory mechanism in turtles. Phys. Zool. 16(3):225–263.

McDowell, S. B., and C. M. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of the Anguinomorphan Lizards. Bull. Amer. Mus. Nat. Hist. 105(1):1–42.

McDowell, S. B. 1972. The evolution of the snakes and its bearing on snake origins. Evol. Biol. 6:191–273.

McKay, W. I. 1889. The osteology amd myology of the death adder (*Acanthrophis antarctica*). Proc. Linn. Soc. New South Wales 4:898–986.

Minot, C. S. 1880. Studies on the tongue of reptiles and birds. Anniv. Mem. Boston Soc. Nat. Hist. 20 pp.

Mitchell, S. W., and G. R. Morehouse. 1863. Researches upon the anatomy and physiology of respiration in the Chelonia. Smithson. Contrib. to Knowledge. 13(159):429.

Mivart, S. G. 1867. Notes on the myology of *Iguana tuberculata.* Proc. Zool. Soc. London. 1867:766–787.

______. 1870. On the myology of *Chamaeleon parsonii.* Proc. Zool. Soc. London. 1870:850–890.

Nash, D. F., and W. W. Tanner. 1970. A comparative study of the head and thoracic osteology and myology of the skinks, *Eumeces gilberti* Van Denburgh and *Eumeces skiltonionus* (Baird and Girard). BYU Sci. Bull., Biol. Ser. 12(2):1–32.

Nick, L. 1913. Das kopfskelett von *Dermochelys coriacea* Linn. Zool. jbb. Abt. Anat. u. Ont. d. Tiere. 33:1–238.

Nonoyama, J. 1936. The distribution of the tastebuds on the tongue of some Reptiles. J. Sci. Hiroshima Univ., Ser B, Dir. 15:57–66.

Norris, K. S., and C. H. Lowe. 1951. A study of the osteology and musculature of *Phrynosoma m'callii* pertinent to its systematic status. Bull. Chicago Acad. Sci. 9:117–125.

Oelrich, T. M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Misc. Publ. Mus. Zool. Univ. Michigan. 94:1–122.

Oldham, J. C., and H. H. Smith. 1975. Laboratory anatomy of the Iguana. Dubuque, Iowa, Wm. C. Brown.

Oldham, J. C., H. M. Smith, and S. A. Miller. 1970. A laboratory prospectus of snake anatomy. Stipes Publishing Co., Champaign, Illinois, 98 pp.

Osawa, G. 1898. Beitrage zur anatomie der *Hatteria punctata.* Archiv. mikroskopische anatomie. 54:481–676.

Parker, W. K. 1880. On the structure and development of the skull in the Lacertilia, Part 1: on the skull of the common lizards *Lacerta agilis, L. viridis,* and *Zootoca vivipara.* Philos. Trans. Royal Soc. London. 170:595–640.

Perrier, E. 1902. Sur l'evolution des formations branchiales chez le lezard et l'orvet. Comptes Rendus Acad. Sci., Paris 135:62–63.

Peyer, B. 1912. Die entwicklung des schadelskelets von *Vipera aspis*. Morph. Jahrb. 44:563–621.

Ping, Chi. 1932. Anatomy of the tongue and its adjacent muscles of *Hemidactylus bouriggii*. Nat. Sci. 8:98–110.

Poglayen-Neuwall, I. 1953. Untersuchungen der Kiefermuskulatur und deren Innervation bei Schildkroten. Acta. Zool. 34:241–292.

———. 1954. Die Kiefermuskulatur der Eidechsen und ihre Innervation. Zeitschrift fur Wissenschaftliche Zoologie. 158:79–132.

Presch, W. 1971. Tongue structure of the teiid lizard genera *Ameiva* and *Cnemidophorus* with a reallocation of *Ameiva vanzoi*. J. Herpetology. 5(3–4):182–185.

Pringle, J. A. 1954. Cranio-development in some South African snakes. Proc. Zool. Soc. London. 123:813–865.

Rao, M. K. M., and L. S. Ramaswami. 1952. The fully formed chondrocranium of *Mabuia* with an account of the adult osteocranium. Acta Zool. 33:209–275.

Rathke, H. 1839. Entwickelungsgechichte der Natter (*Coluber natrix*). Borntrager, Konigsberg.

Rathor, M. S. 1969. The morphology of the Indian sand lizard *Ophiomorus tridactylus* (Blyth) Boulenger. Gengenbaurs Morphol. Jahrb. 114(2):161–168.

Reese, A. M. 1915. The alligator and its allies. G. P. Putnam and Sons, New York and London, 358 pp.

———. 1932. The development of the snake's tongue. Anat. Anz. 74:207–218.

Reese, H. M. 1923. The osteology of the Tegu. *Tupinambis nigropunctatus*. J. Morph. 38:1–17.

Renous, S. 1977. Musculature of the buccal floor of *Bipes canaliculatus* (Reptilia:Amphisbaenia). Copeia 1977(3):464–471.

Renous-Lecuru, S. 1972. Discussion sur les variations du plexis brachial chez deux lacertiliens: *Agama agama* Linn. (Agamides et *Chalarodon madagascariensis* Peters (Iguanides). Gegenbaurs. Morph. Jahrb. 118(1):81–104.

Rice, E. L. 1920. The development of the skull in the skink, *Eumeces guinqialineatus*. Journ. Morph. 34:119–220.

Richter, H. 1933. Das Zungebein und seine Musculatur bei den *Lacertilia vera*. Jena Z. Naturw. 66(3):395–480.

Rieppel, O. 1978. The throat musculature of *Sphenodon*, with comments on the primitive character states of the throat muscles in lizards. Dept. Zool. Nat. Hist. Basel, Switzerland. Anat. Anz. 144:429–440.

———. 1979. A cladistic classification of primitive snakes based on skull structure. Z. Zool. Syst. Evolutions-Forsch. 17(2):140–150.

———. 1981. The hyobranchial skeleton in some little-known lizards and snakes. J. Herpetology 15(4):433–440.

Robison, W. G., and W. W. Tanner. 1962. A comparative study of the species of the genus *Crotaphytus* Holbrook (Iguanidae). BYU Sci. Bull., Biol. Ser. 2(1):1–31.

Romer, A. S. 1956. Osteology of the reptiles. Univ. of Chicago Press, Chicago, 772 pp.

Rosenberg, H. I. 1968. Cephalic anatomy of *Bungarus fasciatus* and morphology of the venom gland of some elapid snakes. Diss. Abstracts. B 29(2):817–818. Univ. microfilms, 68-11:529.

Rosenberg, H. I., and C. Gans. 1976. Lateral head muscles of *Elachistodon westermanni* Reinhardt (Reptilia:Serpentes). Canadian J. Zool. 54(4):510–521.

Saint-Remy, G., and A. Prenant. 1904. Recherches sur le developpement des derives branchiaux chez les sauriens et les ophidiens. Arch. Biol. 20:145–216.

Sanders, A. 1870. Notes on the myology of *Platydactylus japonicus*. Proc. Zool. Soc. London 1870:413–426.

———. 1872. Notes on the myology of *Liolepis belli*. Proc. Zool. Soc. London 1872:154–183.

———. 1874. Notes on the myology of *Phrynosoma cornatum*. Proc. Zool. Soc. London 1874:71–89.

Savage, J. M. 1963. Studies on the lizard family Xantusudae IV, the genera. Contributions in Science, Los Angeles County Museum, No. 71.

Schumacher, G. H. 1956. Kritische Stellungnahme zu der Arbeit von Ivo Poglayen-Neuwall "Untersuchungen der Kiefermuskulatur und deren Innervation bei Schildkroten." Acta Zool. Stockh. 37:1–42.

———. 1973. The head muscles and hyolaryngeal skeleton of turtles and crocodilians. Biology of the Reptilia, Vol. 4, Academic Press, London and New York, 101–199.

Secoy, D. M. 1971. The myology of *Sceloporus clarki clarki* Baird and Girard (Reptilia:Iguanidae). BYU Sci. Bull., Biol. Ser. 14(1):1–22.

Sewertzoff, S. 1929. Zur Entwickiungsgeschichte der zunge bei den Reptilien. Acta Zool. Stockholm. 10:231–341.

Shah, R. V. 1963. The neck musculature of a cryptodire (*Deirochelys*) and a pleurodire (*Chelodina*) compared. Bull. Mus. Comp. Zool. 129(6):343–368.

Sidky, J. A. 1967. The carotid sinus in lizards with an anatomical survey of the ventral neck region. J. Morph. 121(4):311–321.

Siebenrock, F. 1892a. Das Skelettvon *Uroplates fimbriatus* Schneid. Ann. Naturhist. Mus. Wien 8:517–536.

———. 1892b. Zur Kenntniss des Kopfskelettes der Scincoiden, Anguiden und Gerhosaursiden. Ann. Naturhist. Mus. Wien 7:163–195.

———. 1893. Das Skelett von *Brooksesia superciliaris* Kuhl. Sitzungebar Akad. Wiss. Wien 102:205–292.

———. 1894. Skelett der *Lacerta simonyi* Steind. Sitz Ber. Akad. Wiss. Wien 103:205–292.

———. 1895. Das Skelett der Agamiden. Sitz Ber. Akad. Wiss. Wien 104:1,1089–1196.

———. 1898. Über den Bau und die Entwicklung des Zungenbeinapparates der Schildkroten. Ann. Naturhist. Hofmus. Wien 13:424–437.

———. 1899. Über den Kehlkopf und die luftrohre der schildkroten. Akademie der Wissenschaften in Wein. Mathem-Naturw. Class. 108(1):583–595.

———. 1900. Der zungenbeinapparat und kehlkopf sammt luftrohre von *Testudo calcarata* Schneid.

Akademie den wissenschaften in Wien. Mathem-Naturw. Class. 109(1):1–8.

Sinitsin, D. T. 1928. The types of skulls in the family Teiidae. Zool. Anz., Leipzig. 76:232–236.

Smalian, O. 1885. Beitrag zur anatomie des Amphisbaenoiden. Zeitschr. Wiss. Zool. 42:126–202.

Smith, H. M., and R. Warner. 1948. Evolution of the ophidian hyobranchium and its bearing on classification. Herpetologica 4(6):189–193.

Soliman, M. A. 1964. Die Kopfnerven der Schildkroten. Zeitschr. Wiss. Zool. 169:216–312.

Soliman, M. A., and M. A. Hegazy. 1971. The cranial nerves of *Chalcides* ocellatus. II The nervus trigeminus. Bull. Fac. Sci. Cairo Univ. 43:63–98.

Sondhi, K. C. 1958. The hyoid and associated structures in some Indian reptiles. Ann. Zool. Agra. 2(11):155–240.

Stannius, H. 1856. Handbuch der Zootomie. 2. Teil: Die Wirbelthiere. Aufl. Veit und Comp., Berlin.

Sukhanov, V. 1961. Some problems of phylogeny and systems of Lacertilia. Zoologichesku Zhurnal, Moscow.

Tanner, W. W. 1952. A comparative study of the throat musculature of the Plethodontidae of Mexico and Central America. Univ. Kans. Sci. Bull. 34(Pt. 2, No. 10):583–677.

Tilak, R. 1964a. The osteology of *Uromastix hardwickii* (Gray). Zool. Anz. 173:403–426.

_____. 1964b. The hyoid apparatus of *Uromastix hardwickii* (Gray). Sci. Gult. 30(5):244–245.

Toerien, M. J. 1950. The cranial morphology of the California lizard *Anniella pulchra* Gray. South African J. Sci. 46:321–342.

Tornier, G. 1904. Bau und betatigung der kopflappen und halsluftsacke bei Chamaleonen. Zool. Jahrb. Anat. 21:1–40.

Underwood, G. 1967. A contribution to the classification of snakes. British Museum (Natural History) Pub. No. 653, 179 pp.

Van Bourgondien, T. M., and R. C. Bothner. 1969. A comparative study of the arterial systems of some new world Crotalinae (Reptilia:Ophidia). Amer. Midland Nat. 81(1):107–147.

Varkey, A. 1979. Comparative cranial myology of North American natricine snakes. Milwaukee Public Museum. Publ. in Biology and Geology 4, iv, 70 pp. 60 fig.

Versluys, J. 1898. Die mittlere und aussere Ohrsphare der Lacertilia und Rhynchycephalia. Inaug. Dissert. Giessen, Gustave Fisher, Jena 1–247.

_____. 1904. Entwicklung der columella auris bei den Lacertilien. Ein Beitrag zur Kenntniss der *schallaeitenden* Apparate und des Zungebeinbogens bei den Sauropsiden. Zool. Jahrb. Abt. Anat. u. Ont. 19:107–188.

_____. 1936. Kranium and Visceralskelett der Sauropsiden, 1. Reptilien. Handb. d. vgl. Anat. d. Wirbeltiere 6, 1936 herausgeg. von Bolk, Goppert, Kallius, Lubosch. Berlin und Wien.

Walter, F. 1887. Das Visceralskelett und seine Muskulatur bie den einheimischen Amphibien und Reptilien. Jena Zsch. Naturw. 21:1–45.

Watkinson, G. G. 1906. The cranial nerves of *Varanus bivittatus*. Morph. Jahrb. 35:450–472, pls. 11–13.

Weaver, W. G., Jr. 1965. The cranial anatomy of the hognosed snakes (*Heterodon*). Bull. Florida State Mus. 9(7):275–305.

Webb, M. 1951. The cranial anatomy of the South African geckos *Palmatogecko rangei* (Anderson) and *Oedura karroica* (Hewitt). Ann. Univ. Stellenbosch 47A(5):133–165.

Weiner, N. J., and H. M. Smith. 1965. Comparative osteology and classification of the crotaphytiform lizards. Amer. Midl. Nat. 73(1):170–187.

Willard, W. A. 1915. Cranial nerves of *Anolis carolinensis*. Bull. Mus. Comp. Zool. 59:17–116.

Winokur, R. M. 1974. (Abstract) Adaptive modifications of the buccal mucosae in turtles. Am. Zool. 13:1347–8.

Young, E. H. E. 1942. The cranial morphology of the California lizard *Xantusia vigilis*. South African J. Med. Sci. 7th Supplement. 1942:19–32.

Zangerl, R. 1944. Contribution to the osteology of the skull of the Amphisbaenidae. Amer. Midl. Nat. 31(4):417–454.

Zavattari, E. 1908. Materiali per lo studio dell-osso ioide dei sauri. Atti della R. accademia delle Scienze di Torino. 43:706–713.

Zug, G. R. 1971. The distribution and patterns of the major arteries of the iguanids and comments on the intergeneric relationships of iguanids (Reptilia:Lacertilia). Smithsonian Contrib. Zool. 85:1–23.

WESTERN DIAMONDBACK RATTLESNAKE IN SOUTHERN NEVADA: A CORRECTION AND COMMENTS

Frederick H. Emmerson[1]

ABSTRACT.— Reports of the occurrence of *Crotalus atrox* Baird & Girard from Nevada are reviewed. There is no evidence to support the occurrence of this species in Nevada.

Andersen and Emmerson (1970, Great Basin Nat. 30:107) reported the taking of a single specimen of western diamondback rattlesnake, *Crotalus atrox* Baird & Girard, from west of the Colorado River in Clark County, Nevada.

The snout-vent length was erroneously reported as "163 mm," permitting the inference that a breeding population may have been present in the Searchlight area, resulting in the collection of a neonate. In fact, the specimen (Univ. of Nevada, Las Vegas R5118) was an adult male with a snout-vent length of 1054 millimeters.

During the years subsequent to the above-cited report, and as recently as 1979, a number of representations were made to me that "diamondbacks" had been taken or seen in Clark County. Inasmuch as no one making the claims produced a specimen of *C. atrox*, nor was any report offered by a competent observer, I concluded that the reports were fictitious or were based upon sightings of *C. mitchelli* or *scutulatus*. I suggest, therefore, that caution be exercised in considering *Crotalus atrox* as part of the Clark County, Nevada, herpetofauna, at least until a series of specimens is at hand.

---

[1] Utica Zoo, Steele Hill Road, Utica, New York 13501.

PREVALENCE OF *ELAEOPHORA SCHNEIDERI* AND *ONCHOCERCA CERVIPEDIS* IN MULE DEER FROM CENTRAL UTAH

Lauritz A. Jensen[1], Jordan C. Pederson[2], and Ferron L. Andersen[1]

ABSTRACT.— Thirteen of 265 deer (4.9 percent) from central Utah were positive for *Elaeophora schneideri*, and 180 (67.9 percent) were infected with *Onchocerca cervipedis*. The rate of infection for *E. schneideri* and *O. cervipedis* increased significantly with age of the host (chi-square of 17.5 and 15.5, respectively, $p < 0.005$). The lack of elaeophorosis in elk from the region is presumably due to the low density of the parasite in mule deer.

The arterial worm (*Elaeophora schneideri*) is enzootic in mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), and other ruminants in the Rocky Mountain area (Hibler and Adcock 1971, Worley 1975), although the prevalence and geographic distribution in Utah is largely undetermined. From 1978 to 1981 biologists of the Utah Division of Wildlife Resources (DWR) identified the arterial worm in one calf and one bull elk from southern Utah and detected microfilariae of *E. schneideri* in 19 of 37 mule deer from the same locality (Coles 1982, pers. comm.). Additionally, from 1978 to 1981 DWR personnel recovered the filarial nematode in three blind moose and one moose with normal sight in northern Utah (Babcock 1982, pers. comm., Kimball 1982, pers. comm.). In contrast, of 23 adult elk and seven calves examined by the authors and DWR officers in central Utah during summer 1981, none manifested clinical signs of elaeophorosis (unpubl. data).

Mule deer are apparently the normal definitive host for *E. schneideri*, and the adult worms are predominately located in the arteries of the neck. Elk and moose, on the other hand, represent abnormal hosts, and are severely affected by the larval stages found in the cephalic arteries, arterioles, and capillaries. Heavily infected elk calves frequently die 7 to 10 days after infection (Hibler 1981). Other symptoms of elaeophorosis in elk and moose include damage to the central nervous system, nystagmus, blindness, cropping of the ears, deformity of the antlers, necrosis of the muzzle and nostrils, and emaciation (Hibler and Adcock 1971, Worley et al. 1972).

The legworm (*Onchocerca cervipedis*) is another filarial nematode enzootic in mule deer in the Rocky Mountains (Walker and Becklund 1970). Adults of the legworm may cause inflammation in the subcutaneous tissue (Wehr and Dikmans 1935); however, infections generally are not clinically significant (Senger 1963). The present study was undertaken to determine the occurrence of *E. schneideri* and *O. cervipedis* in deer from central Utah.

Samples of skin from the muzzle of 265 deer were macerated in physiological saline and examined for microfilariae of *E. schneideri* and *O. cervipedis* following generally the procedure described by Weinmann et al. (1973). The animals were hunter-killed in autumn 1981 in the counties of Carbon, Duchesne, Emery, Juab, Sanpete, Utah, and Wasatch.

Thirteen of the 265 deer (4.9 percent) were positive for *E. schneideri* and 180 (67.9 percent) were infected with *O. cervipedis* (Table 1). Deer positive for both parasites were recovered from all counties listed above. The rate of infection for the arterial worm and the legworm increased significantly with age of the host (chi-square of 17.5 and 15.5, respectively, $p < 0.005$).

The apparent lack of elaeophorosis in elk in central Utah may be related to the low density of the parasite in mule deer from the region. The high rate of infection for both species of roundworms demonstrated in older

---

[1] Department of Zoology, Brigham Young University, Provo, Utah 84602.

[2] Utah Division of Wildlife Resources, 1115 North Main, Springville, Utah 84663.

TABLE 1. Prevalence of *Elaeophora schneideri* and *Onchocerca cervipedis* in mule deer from Central Utah.

Age of deer	Number of deer examined	Deer infected with *E. schneideri*		Deer infected with *O. cervipedis*	
		Number	Percent	Number	Percent
Yearlings	175	2	1.1	105	60.0
2–3 years	27	2	7.4	21	77.8
>3 years	63	9	14.3	54	85.7
Total	265	13	4.9	180	67.9

animals is presumably related to the time of exposure in the enzootic area. Yearlings are apparently not refractory to either parasite.

Voucher specimens: microfilariae of *E. schneideri* and *O. cervipedis* USNM Helm. Coll. No 76931.

ACKNOWLEDGMENTS

Thanks are given to Holly Betteridge, Harold Blackburn, Brad Bradly, Paul Tervort, and Dick Worthen, Division of Wildlife Resources, Utah, for assisting with the collecting of the samples. We are indebted to Dr. Charles P. Hibler, Wild Animal Disease Center, Colorado State University, for confirming the identifications of the microfilariae. Appreciation is also extended to Kimball T. Harper, Rodney T. John, and Bruce L. Welch for their suggestions in the preparation of this manuscript.

LITERATURE CITED

BABCOCK, W. H. 1982. [Letter to Jordan C. Pederson]. Located at: Utah Division of Wildlife Resources, Springville, Utah.

COLES, F. H. 1981. [Letter to Jordan C. Pederson]. Located at: Utah Division of Wildlife Resources, Springville, Utah.

HIBLER, C. P. 1981. Elaeophorosis. Pages 53–59 *in* W. J. Adrian, ed., Manual of common wildlife diseases in Colorado. Colorado Division of Wildlife.

HIBLER, C. P., AND J. L. ADCOCK. 1971. Elaeophorosis. Pages 263–278 *in* J. W. Davis and R. C. Anderson, eds., Parasitic diseases of wild mammals. Iowa State Univ. Press, Ames, Iowa.

KIMBALL, J. F. 1982. [Letter to Lauritz A. Jensen]. Located at: Utah Division of Wildlife Resources, Springville, Utah.

SENGER, C. M. 1963. Some parasites of Montana deer. Montana Wildl. Autumn: 5–13.

WALKER, M. L., AND W. W. BECKLUND. 1970. Checklist of the internal and external parasites of deer, *Odocoileus hemionus* and *O. virginianus*, in the United States and Canada. Special Publication No. 1, Index-Catalogue of Medical and Veterinary Zoology, U.S. Govt. Print. Off., Washington, D.C.

WEHR, E. E., AND G. DIKMANS. 1935. New nematodes (Filariidae) from North American ruminants. Zool. Anz. 110:202–208.

WEINMANN, C. J., J. R. ANDERSON, W. M. LONGHURST, AND G. CONNOLLY. 1973. Filarial worms of Columbian black-tailed deer in California. 1. Observations in the vertebrate host. J. Wildl. Dis. 9:213–220.

WORLEY, D. E. 1975. Observations on epizootiology and distribution of *Elaeophora schneideri* in Montana ruminants. J. Wildl. Dis. 11:486–488.

WORLEY, D. E., C. K. ANDERSON, AND K. R. GREER. 1972. Elaeophorosis in moose from Montana. J. Wildl. Dis. 8:242–244.

ECOMORPHOLOGY AND HABITAT UTILIZATION OF *ECHINOCEREUS ENGELMANNII* AND *E. TRIGLOCHIDIATUS* (CACTACEAE) IN SOUTHEASTERN CALIFORNIA

Richard I. Yeaton[1]

Abstract.— The relationship between form and habitat utilization of *Echinocereus engelmannii* and *E. triglochidiatus* was studied in southeastern California. The major difference in form is in the density of stems comprising the canopy. These differences in morphology create differences in the daily heat loads of each species. *Echinocereus triglochidiatus,* with its stems densely packed and in contact with each other over much of their lengths, continues to gain heat internally as the sun sets due to conductance between the stems. In contrast *E. engelmannii,* with a more open canopy, begins to lose heat as the sun goes down. As a result, *E. triglochidiatus* is successful in the juniper-pinyon zone where winter temperatures are cold for long periods and *E. engelmannii* is more successful in the lower desert regions where very hot, summer temperatures prevail. In the latter case, daytime buildup in heat load is reduced by convective cooling as air moves through the open canopy. Differences in microhabitat utilization occur that provide a second mechanism to reduce daily heat load buildup on hot summer days in the juniper-pinyon zone.

Plants in their natural habitats must cope with the environmental variations experienced in each microhabitat. A series of adaptive strategies, which involves gaining access to sufficient water, nutrients, and light for maintenance, growth and reproduction while at the same time avoiding the effects of desiccation and extreme temperatures that can lead to mortality, is used to achieve this (e.g., Gates 1962). Nowhere are these strategies more apparent than in plants occupying extreme environments. In particular, most morphological aspects of members of the Cactaceae have been suggested as representing ecological strategies for their successful adaptations to hot, dry environments (Gates 1962, Felger and Lowe 1967, Nobel 1978, 1980a, Yeaton et al. 1980).

The literature on problems of adaptations in form for Cactaceae involves two types of studies; one in which access to sufficient light for photosynthesis is considered (Rodriquez et al. 1976, Nobel 1980b, Yeaton et al. in review) and the other in which avoidance of extreme temperatures, particularly freezing temperatures, is emphasized (Felger and Lowe 1967, Gibbs and Patten 1970, Mozingo and Comanor 1975, Nobel 1978, 1980a). Two extremes in the form of Cactaceae parallel this division. When access to light is discussed, platyopuntias, a group with flattened cladodes, are usually studied. In contrast, when temperature is a problem, the growth form of the species studied is usually some variant of a cylinder.

In this study, the relationship between heat load and habitat utilization is examined for two species of *Echinocereus* that are morphological variants of the cylindrical form. *Echinocereus engelmannii* (Parry) Lemaire is found on rocky slopes of elevations of 600–1500 m in the Mojave Desert of California (Benson 1969). It is caespitose with 5 to 60 stems forming an open mound. The second species, *Echinocereus triglochidiatus* Engelm., is found at somewhat higher elevations (1000–2500 m) above the deserts, usually in the juniper-pinyon woodland (Benson 1969). It also has a caespitose form with multiple stems forming a dense mound. The compactness of stems in the mounds is the most striking difference in form between the two species and results in a lower effective surface-to-volume ratio in *E. triglochidiatus.* I concentrated on this morphological dissimilarity (1) to determine what differences occur in the daily heat load experienced by individuals of each species and (2) to explain differences in habitat utilization by each species.

---

[1] Centro de Botánica y Centro Regional para Estudios de Zonas Aridas y Semiáridas, Colegio de Postgraduados, Chapingo, Edo. de Mexico, Mexico. Present address: Molecular Biology Institute, UCLA, Los Angeles, California 90024.

Study Areas and Methods

A population of *Echinocereus engelmannii* was studied at Hole-in-the-Wall at the base of the Providence Mountains in the Mojave Desert of southeastern California (latitude 35°3′ N, longitude 115°23′ W). For a description of this site, see Yeaton and Cody (1979). Populations of *E. engelmannii* and *E. triglochidiatus* were studied in the juniper-pinyon zone (latitude 35°4′ N, longitude 115°28′ W). Here rainfall is more abundant and average maximum daily temperatures are lower (Oosting 1956, Trombulak and Cody 1980). As a result, snow is common during the months of December, January, and February and persists for several days or weeks, in contrast to the lower desert site. At the upper site the dominant vegetation consists of *Artemisia tridentata*, *Juniperus monosperma*, and *Pinus monophylla*.

At each study site, all individuals of *E. engelmannii* and *E. triglochidiatus* were categorized according to the kind of microhabitat utilized. The characteristics of these microhabitats were quantified from the perspective of the plant. Three general microhabitats may be distinguished at the juniper-pinyon site: rocky slope, composed of a mosaic of boulders and gravel and found at slope angles greater than 8 degrees; under juniper and pinyon, generally at slope angles less than 8 degrees; and washes, disturbed areas with *Artemisia tridentata* dominating the plant community. At the desert study site, only the rocky slope microhabitat is utilized extensively, washes are rarely colonized by *Echinocereus* (possibly due to greater effects of erosion), and no counterpart to juniper-pinyon canopy exists. The following microhabitat characteristics were recorded for each *Echinocereus* individual whenever possible: slope aspect (either north-facing [270–90 degrees] or south-facing [90–270 degrees]), shaded or unshaded by adjacent rocks or plants. These data were organized into contingency tables with row headings consisting of the two species of *Echinocereus* and column headings describing the contrasting characteristics of each microhabitat. Entries into the tables were the numbers of individuals encountered in each situation. Totals from table to table were not necessarily equivalent because some individuals could not be assigned to a particular category. Either Chi-square or Fisher Exact Probability tests were employed to determine differences in microhabitat utilization between the two species (Siegel 1956).

Table 1. Habitat utilization by individuals of *Echinocereus triglochidiatus* and *E. engelmannii* in the juniper-pinyon zone of the Providence Mountains, California.

Species	Rocky slopes	Pinyon pine or wash
E. triglochidiatus	65	39
E. engelmannii	38	0

Fisher Exact Probability Test, $p < 0.001$.

The sizes of the 10 largest individuals of each species in each microhabitat were measured. Because both species form mounds that are roughly hemispherical in shape, one approximation of size is the diameter of the mound. A second measure of size is the number of stems comprising each mound. To describe the degree of openness of the canopy of each individual, a ratio of the number of stems divided by the mound diameter was calculated and compared by means of a Student's t-test (Steel and Torrie 1960). In addition, the diameters of one stem from 25 individuals of each species were measured and tested similarly.

Daily temperature regimes were measured for a large (0.5 m diameter) individual of each species that had been transplanted into a shallow clay pot and removed to an open site where the plant would not be shaded over the course of a day. The two species were set side-by-side and a Yellowsprings Instrument Tele-thermometer and probes were used to simultaneously record hourly ambient air temperature, cactus surface temperatures (on the east-facing side of the center stem), and internal stem temperatures (at 6 cm and 10 cm depths in the center stem of each individual). These temperatures are plotted for 15 September 1980 and are used to illustrate the differences in daily heat loads due to degree of openness of the canopy. Graphs were made of the daily course of the ambient air temperatures and the differences between ambient temperatures and surface and internal temperatures for each species.

Results

At the desert site, only individuals of *Echinocereus engelmannii*, utilizing rocky slope microhabitats, are found. At the juniper-pinyon site, individuals of both species occur. At this site *E. engelmannii* is found only in the rocky slope microhabitat, but *E. triglochidiatus* is found in all three microhabitats (Table 1). At the juniper-pinyon site, *E. engelmannii* is located on south-facing slopes only, but individuals of *E. triglochidiatus* are equally divided between north- and south-facing slopes (Table 2). *Echinocereus engelmannii* apparently requires open, sunny microhabitats for successful establishment, but *E. triglochidiatus* is favored by more shaded, northern exposures. This distinction is further illustrated by the characteristics of microhabitat involving shading. *E. engelmannii* is almost always found in unshaded microhabitats, but *E. triglochidiatus* is found in shaded situations, whether it occurs on north- or south-facing slopes (Table 3).

The means and standard errors for size measurements of the 10 largest individuals of each species in each microhabitat are given in Table 4. Comparison of the mean values for mound diameters and number of stems between the two species on the rocky slope at the juniper-pinyon site shows that *E. triglochidiatus* is much larger than *E. engelmannii* (for diameter $t = 6.54$, d.f. $= 18$, $p < 0.001$; for number of stems $t = 10.23$, d.f. $= 18$, $p < 0.001$). These differences combine to give significantly lower mean values for the ratio of stem number/mound diameter for *E. engelmannii*, indicating that the spacing between stems is relatively large ($t = 12.58$, d.f. $= 18$, $p < 0.001$). This is not due to differences in stem diameter because no significant difference was found between the two species (for *E. engelmannii* stem diameter $\bar{x} \pm$ S.E. $= 5.18$ cm ± 0.16; for *E. triglochidiatus* $\bar{x} \pm$ S.E. $= 4.82$ cm ± 0.15; $t = 1.63$, d.f. $= 48$, $0.2 < p < 0.1$). No difference in the stem number/mound diameter ratio exists between the upper and lower populations of *E. engelmannii*; however individuals of the upper population are significantly smaller in diameter ($t = 6.06$; d.f. $= 18$, $p < 0.001$) and in stem number ($t = 6.38$, d.f. $= 18$, $p < 0.001$) than are individuals measured at the desert site. For *E. triglochidiatus* a gradual reduction in diameter and stem number and an increase in the openness of the canopy occurs from the rocky slope through the juniper-pinyon to the washes (Table 4). The only significant differences occur between the rocky slope and wash microhabitats for this species (for mound diameter $t = 2.47$, $p < 0.05$; for stem number $t = 4.48$, $p < 0.001$; for the ratio $t = 3.53$, $p < 0.01$; d.f. $= 18$ in all cases).

The daily temperature regimes are shown in Figure 1. Ambient air temperature increases from early morning until late afternoon and decreases as the sun sets (Fig. 1a). For the relatively open-canopied *E. engelmannii*, surface temperatures are much greater during the early part of the day and decrease rapidly as the east-facing side of the stem is shaded in the later daylight hours (Fig. 1b). At the 6 cm depth, temperatures appear buffered and fluctuate around the ambient temperature during the day, heating up as the sun goes down (Fig. 1b). At the 10 cm depth, temperatures start below ambient in the morning, increase rapidly during the day, and gradually decrease in the evening (Fig. 1b). In contrast, the closed-canopied *E. triglochidiatus* maintains surface and internal stem temperatures below those of ambient during the daylight hours and gradually increase as the sun sets. By midnight, temperatures in *E. triglochidiatus* stems are greater than those for *E. engelmannii* under the same conditions (Fig. 1c).

Table 2. Slope aspect utilization for individual of *Echinocereus triglochidiatus* and *E. engelmannii* in the juniper-pinyon zone of the Providence Mountains, California.

Species	North-facing (270–90 degrees)	South-facing (90–270 degrees)
E. triglochidiatus	23	24
E. engelmannii	2	33

Fisher Exact Probability Test, $p < 0.001$.

Discussion

Felger and Lowe (1967) described changes in the form of *Lophocereus schottii* over a latitudinal gradient, with a tendency for larger diameter and a reduced number of stem ribs toward the colder, northern edges of its distribution. Also Niering, Whittaker, and Lowe (1963) demonstrated an increase in the diameter of *Carnegica gigantea* at the northern limits of its distribution. These changes have the effect of reducing the surface-to-volume ratio and increasing the time lag before the tissues suffer damages from freezing temperatures, as has been simulated by Lewis and Nobel (1977) and Nobel (1978). These changes occur within species, but the results may be extrapolated to those observed for the two species of *Echinocereus*. In form, *E. triglochidiatus* has a more closed canopy than does *E. engelmannii*, because its stems grow in contact with one another. Hence its surface-to-volume ratio is reduced, and the species approximates in form a solid cylinder or "barrel." *Echinocereus triglochidiatus* is found only at the juniper-pinyon site where exposure to freezing temperatures at night can be a severe problem. The time lag, in which the internal stem temperatures are still increasing because of conductance between stems after the sun sets, may enable *E. triglochidiatus* to survive low night temperatures. In contrast, *E. engelmannii* may be unable to survive low night temperatures due to its more open growth form. As a result, it is only established at the colder juniper-pinyon site on unshaded, south-facing rocky slopes. Here it can warm up rapidly in the morning, minimizing the time during which its tissues are exposed to freezing temperatures. Its growth form at the juniper-pinyon site, rather than approximating the compactness of *E. triglochidiatus*, is open due to the hot summer temperatures experienced in this microhabitat. The smaller maximum size, attained by *E. engelmannii* at the juniper-pinyon site, is probably the result of its establishment at the extreme upper limits of its elevational range, where its growth rate is slower and less constant and its probability of survival to the maximum sizes attained at the desert site is very low. At the desert site, freezing temperatures are less of a problem. High summer temperatures appear to be more critical there. One way of reducing the heat load of an individual is to open the canopy, permitting convective cooling as air moves through the canopy.

Table 3. Shade utilization by individuals of *Echinocereus triglochidiatus* and *E. engelmannii* in the juniper-pinyon zone of the Providence Mountains, California.

Species	Shade	No shade
E. triglochidiatus	67	5
E. engelmannii	5	38

$x^2 = 72.8$ $p < 0.01$.

Although morphology appears to be an adaptation to the extremes in temperature that *Echinocereus* experiences, each species must cope with problems posed when the opposite climatic conditions occur. For example, hot summer days do occur at the juniper-pinyon site and freezing winter nights do occur at the desert site, although at a reduced frequency in comparison with their opposite extremes. Microhabitat differences become important in moderating the heat load and exposure to freezing temperatures. During the hot summer months, when the sun is directly overhead at midday, *E. triglochidiatus* is usually in the shade. Its daily heat load is reduced, because ambient temperatures in the shade are lower (Bannister 1976, Yeaton et al., in review). Conversely, in the winter months, when the sun is at a lower angle, *E. triglochidiatus* may be in direct sunlight during part of the day. At the desert site, *E. engelmannii* may avoid the effects of freezing temperatures by using unshaded microhabitats in which individual stems can heat rapidly in the early morning as the sunlight strikes them.

One comment should be made about the temperature measurements made. The great difference in surface temperature, recorded in the morning hours, is the direct result of differences in the canopy structure for the two species. As a result of its more open canopy, the stems of *E. engelmannii* are exposed at times to direct sunlight and heat more rapidly than do the stem surfaces of the closed-canopied *E. trigiochidiatus*, which are always shaded. For this reason surface and internal temperatures of *E. triglochidiatus* fluctuate similarly over the course of the day, and

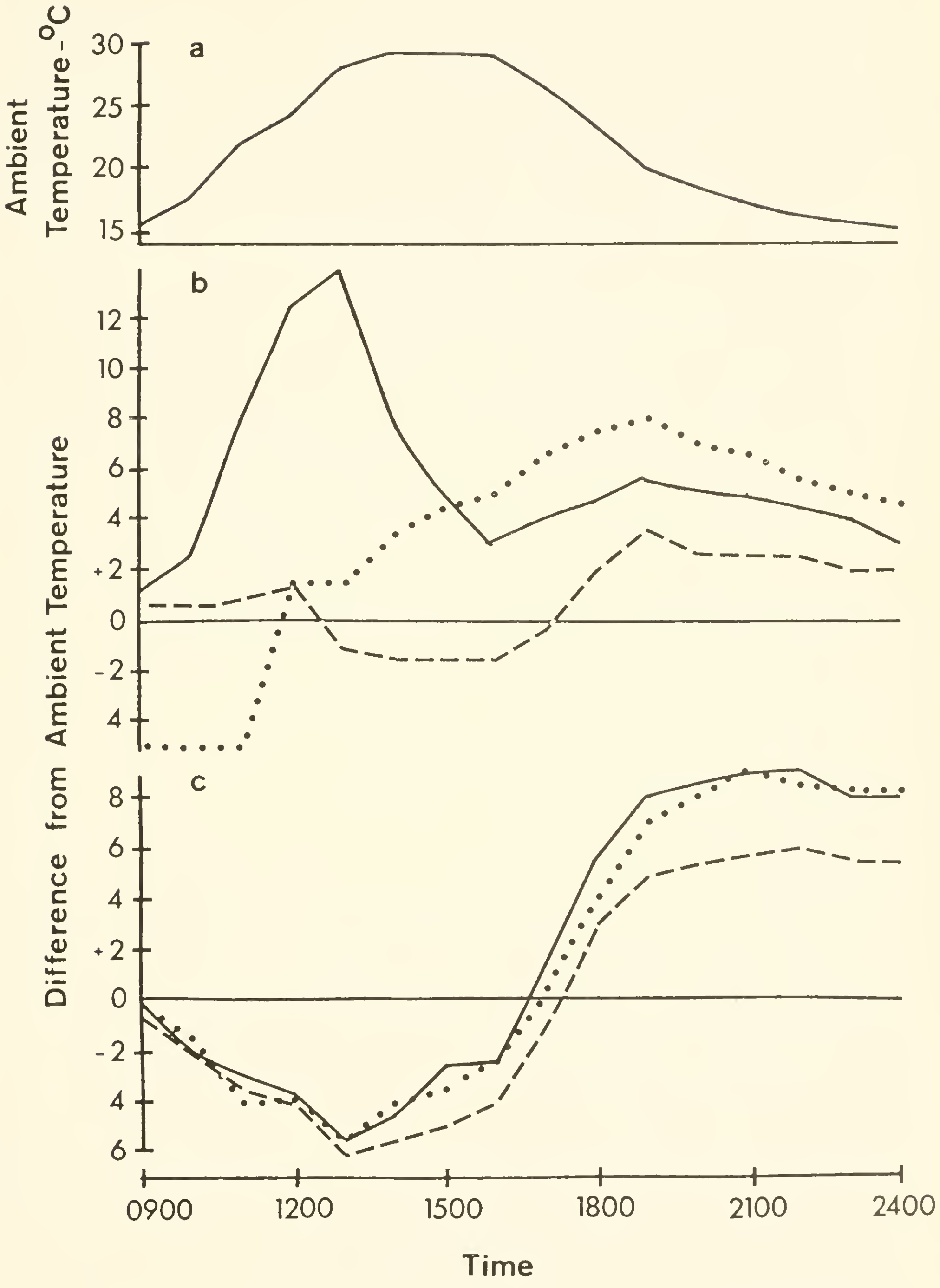


Fig. 1. The relationship between ambient temperature and surface and internal stem temperatures for transplanted *Echinocereus engelmannii* and *E. triglochidiatus* in an open site over a 15-hour period on 15 September 1980. (a), Ambient air temperatures; (b), The differences from ambient temperature for surface (______), 6 cm deep (------), and 10 cm deep (......) probes in or on the central stem of *E. engelmannii*; (c), the same as b. but for *E. triglochidiatus*.

TABLE 4. Means and standard errors for size measurements of the 10 largest individuals of *Echinocereus triglochidiatus* and *E. engelmannii* found in each habitat utilized in the juniper-pinyon and desert zones of Providence Mountains, California.

Habitat	Diameter (cm)	No. Stems	No. Stems/Diameter	Individual Stem Diameter (mm)
Juniper-pinyon				
E. triglochidiatus—Rocky	45.20 ± 3.60	86.40 ± 7.44	1.93 ± 0.10	5.18 ± 0.16
—Pinyon	39.50 ± 4.50	76.40 ± 11.55	1.77 ± 0.17	
—Wash	34.50 ± 2.41	47.60 ± 4.43	1.41 ± 0.11	
E. engelmannii —Rocky	19.20 ± 1.69	10.00 ± 0.67	0.55 ± 0.05	
Desert				
E. engelmannii —Rocky	47.20 ± 4.30	30.30 ± 3.11	0.67 ± 0.07	4.82 ± 0.15

widely divergent temperatures are recorded in the same period for *E. engelmannii*. The difference in surface temperature is further exacerbated by the differential movement of air through the canopies of the two species, resulting in different rates of convective cooling. Thus, surface temperatures may not be compared with the internal stem temperatures except as general trends. This is because the temperatures recorded on the surface are a direct response to environmental conditions, but the internal stem temperatures represent various degrees of integration of these same environmental conditions. The internal stem temperatures may be compared between the 6 cm and 10 cm depths and, as would be expected, the 10 cm depth becomes warmer than the 6 cm depth as the day progresses.

I have concentrated in this study on the differences in form of two species of *Echinocereus*. Other differences such as spine coverage, spine color, apical pubescence, and tissue thermal properties have been demonstrated as being important in the regulation of heat load in Cactaceae (Nobel 1978). Differences between the two species do exist for some of these characteristics (Benson 1969). *Echinocereus engelmannii* is more heavily spined and its spines are lighter colored than those of *E. triglochidiatus*. Also, the central spines of *E. engelmannii* are flattened in contrast to those of *E. triglochidiatus*. These factors contribute to its adaptation to unshaded microhabitats by increasing its albedo (Gibbs and Patten 1970, Nobel 1978). Additionally, *E. triglochidiatus* has permanent apical pubescence on mature stems, but *E. engelmannii* loses its pubescence after 2–3 years. Apical pubescence may have an insulative effect (Nobel 1978), which may be important in survival of stems of *E. triglochidiatus* in cold habitats. I have no information on the thermal properties of stem tissues.

Thus, the differences in morphology observed in *Echinocereus engelmannii* and *E. triglochidiatus* appear to be adaptations for avoidance of extreme climatic conditions in their preferred habitats, and differences in microhabitats enable the individual to avoid the opposite extremes should they occur. In other words, the constraints imposed by morphology are ameliorated by differences in microhabitat use.

ACKNOWLEDGMENTS

I thank R. W. Eckert, W. Work, and R. W. Yeaton for their assistance in this study.

LITERATURE CITED

BANNISTER, P. 1976. Introduction to physiological plant ecology. Halstead Press, New York.

BENSON, L. 1969. The native cacti of California. Stanford Univ. Press, Stanford.

FELGER, R. W., AND C. H. LOWE. 1967. Clinal variation in the surface-volume relationships of the columnar cactus *Lophocereus schottii* in northwestern Mexico. Ecology 48:530–536.

GATES, D. M. 1962. Energy exchange in the biosphere. Harper and Row, New York.

GIBBS, J. G., AND D. T. PATTEN. 1970. Plant temperatures and heat flux in a Sonoran Desert ecosystem. Oecologia 5:165–184.

LEWIS, D. A., AND P. S. NOBEL. 1977. Thermal energy exchange model and water loss of a barrel cactus, *Ferocactus acanthodes*. Plant Physiology 60:609–616.

Mozingo, H. N., and P. L. Comanor. 1975. Implications of the thermal response of *Ferocactus acanthodes*. Supplement of the Cactus and Succulent J. (U.S.):22–28.

Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The saguaro: a population in relation to environment. Science 142:15–23.

Nobel, P. S. 1978. Surface temperatures of cacti: influences of environmental and morphological factors. Ecology 59:986–996.

______. 1980a. Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran Desert. Ecology 61:1–7.

______. 1980b. Interception of photosynthetically active radiation by cacti of different morphology. Oecologia 45:160–166.

Oosting, H. J. 1956. The study of plant communities. W. H. Freeman and Co., San Francisco.

Rodriquez, S. B., F. B. Perez, and D. D. Montenegro. 1976. Eficiencia fotosintetica del nopal (*Opuntia* spp.) en relación con la orientación de sus cladodes. Agrociencia 24:67–77.

Siegel, S. 1956. Non-parametric statistics. McGraw-Hill, New York.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

Trombulak, S. C., and M. L. Cody. 1980. Elevational distribution of *Pinus edulis* and *P. monophylla* (Pinaceae) in the New York Mountains, eastern Mojave Desert, Madroño 27:61–67.

Yeaton, R. I., and M. L. Cody. 1979. The distribution of cacti along environmental gradients in the Sonoran and Mojave deserts. J. Ecology 67:529–541.

Yeaton, R. I., R. Karban, and H. Wagner. 1980. Morphological growth patterns of Saguaro (*Carnegiea gigantea*: Cactaceae) on flats and slopes in Organ Pipe Cactus National Monument, Arizona. Southwestern Nat. 25:339–349.

Yeaton, R. I., E. B. Layendecker, K. S. Sly, and R. W. Eckert. Some aspects of microhabitat differences between two species of cactus in the mixed Chaparral-Inland Coastal Sage Association of southern California. In review.

FIRST SPECIMEN OF THE SPOTTED BAT (*EUDERMA MACULATUM*) FROM COLORADO

Robert B. Finley, Jr.,[1] and James Creasy[2]

Abstract.— A spotted bat (*Euderma maculatum*) was picked up at the headquarters of Browns Park National Wildlife Refuge, Moffat County, Colorado, on 29 August 1981.

The spotted bat (*Euderma maculatum*) has not been reported from Colorado, although its presence in the state was considered probable by Armstrong (1972). The specimen reported here was an accidental find, like many others previously reported (Barbour and Davis, 1969).

On 29 August 1981, at about 1000 MDT on a clear day, Creasy found an adult female spotted bat resting on a concrete slab behind the shop in the old headquarters area of the Browns Park National Wildlife Refuge, 1630 m, Moffat County, Colorado. When touched, it spread its wings, raised its head and ears, and opened its mouth, but made no effort to fly. It was prepared as a study skin, skull, and alcoholic carcass; no sign of injury or illness was found during preparation. It was deposited in the Biological Surveys collection at Fort Collins (BS/FC 7557).

Browns Park is a wide, mountain-ringed valley or "park" about 25 km long, through which the Green River meanders before entering Gates of Lodore, a narrow gorge at the north end of Dinosaur National Monument. The headquarters site is 9 km north and 2 km west of Gates of Lodore, on a strip of cottonwood bottom between the left bank of the Green River and Harry Hoy Bottom, a cattail-bulrush marsh. The nearest cliffs are on the steep rocky mountainside 3 km southwest across the Green River. Cliffs a few hundred meters high form the walls of the Gates of Lodore 10 km to the south. The rocky mountainsides encircling Browns Park are wooded with pinyon-juniper.

The nearest locality previously reported for the spotted bat was Salt Lake City, Utah, approximately 255 km to the west (Durrant 1935). Nearest known localities in other directions are 5 mi NW Monticello, Utah, approximately 355 km to the south (Benson 1954); and Byron, Bighorn Co., Wyoming, approximately 440 km to the north (Mickey 1961).

External measurements (in millimeters) of the specimen from Browns Park NWR are: total length, 119; length of tail, 53; length of hind foot, 13; length of ear, 42; length of tragus, 15; width of tragus, 5; length of forearm, 52; and weight, 13.5 g. Cranial measurements (in mm) taken as described by Handley (1959) are: greatest length of skull, 19.4; zygomatic breadth, 10.7; interorbital breadth, 4.2; breadth of braincase, 9.4; depth of braincase, 5.7; maxillary toothrow, 6.3; postpalatal length, 8.1; and palatal breadth, 7.2.

Literature Cited

Armstrong, D. M. 1972. Distribution of mammals in Colorado. Mono. Mus. Nat. Hist., Univ. of Kans. 3. 415 pp.

Barbour, R. W., and W. H. Davis. 1969. Bats of America. Univ. Press of Kentucky. 286 pp.

Benson, S. B. 1954. Records of the spotted bat (*Euderma maculata*) from California and Utah. J. Mamm. 35(1):117.

Durrant, S. D. 1935. Occurrence of the spotted bat in Utah. J. Mamm. 16(3):226.

Handley, C. O., Jr. 1959. A revision of the American bats of the genera Euderma and Plecotus. Proc. U.S. Natl. Mus. 110:95–246.

Mickey, A. B. 1961. Record of the spotted bat from Wyoming. J. Mamm. 42(3):401.

---

[1] U.S. Fish and Wildlife Service, 1300 Blue Spruce Drive, Fort Collins, Colorado 80524-2098.

[2] Browns Park National Wildlife Refuge, Greystone Route, Maybell, Colorado 81640.

STATUS OF INTRODUCED FISHES IN CERTAIN SPRING SYSTEMS IN SOUTHERN NEVADA

Walter R. Courtenay, Jr.,[1] and James E. Deacon[2]

Abstract.— We record eight species of exotic fishes as established, reproducing populations in certain springs in Clark, Lincoln, and Nye counties, Nevada. These include an unidentified species of *Hypostomus*, *Cyprinus carpio*, *Poecilia mexicana*, *Poecilia reticulata*, a *Xiphophorus* hybrid, and *Cichlasoma nigrofasciatum*. *Tilapia mariae*, established in a spring near the Overton Arm of Lake Mead, and *Tilapia zilli*, established in a golf course pond in Pahrump Valley, are recorded for the first time from Nevada waters. Though populations of transplanted *Gambusia affinis* persist, other populations of *Poecilia latipinna* are apparently no longer extant. *Cichlasoma severum*, *Notemigonus crysoleucas*, *Poecilia latipinna*, and *Carassius auratus* were apparently eradicated from Rogers Spring in 1963.

Miller and Alcorn (1943), Miller (1961), La Rivers (1962), Deacon et al. (1964), Hubbs and Deacon (1964), Minckley and Deacon (1968), Minckley (1973), Hubbs et al. (1974), Deacon (1979), Hardy (1980), and others recorded the presence of non-native fishes in Nevada. In those papers, it was stressed that the introduction of nonnative fishes, be they exotic (of foreign origin) or transplants native to other areas of the United States, can have serious, adverse impacts on the depauperate and often highly endemic fish fauna in the southwestern U.S. Deacon et al. (1964) emphasized that most of the endemic fishes are small and, therefore, subject to more adverse impacts through introductions of small bait or ornamental fishes than with earlier introductions of larger fishes, a subject reviewed by Hubbs and Broderick (1963).

In this paper, we document eight species of exotic fishes in three counties of southern Nevada. One of these fishes, the spotted tilapia (*Tilapia mariae*), was previously known to have become established only in Florida (Hogg 1974, 1976, Courtenay and Robins 1975, Courtenay 1979b, 1980, Courtenay and Hensley 1979, 1980). Another, the redbelly tilapia (*Tilapia zilli*), has been recorded as established in Arizona, California, and Texas (Courtenay and Hensley 1980). Our purpose is to update the status of introduced fishes in southern Nevada, primarily from the reports of Deacon et al. (1964) and Hubbs and Deacon (1964).

Clark County

Indian Spring is 2 km south of U.S. Highway 95, approximately 62 km northwest of Las Vegas in the village of Indian Springs. Minckley (1973) recorded a suckermouth catfish (*Hypostomus*) as successfully established since at least 1966 "in a warm spring in southern Nevada"; this reference was to Indian Spring. Brief examination of Indian Spring by Deacon since 1966 demonstrates that the population has remained common and continues to reproduce successfully. The deeply undercut banks with numerous tree roots and holes provide excellent refuge for this rather cryptic species. Our collection on 18 October 1980 yielded only one specimen, despite repeated seining. A local resident advised us that local youngsters had removed as many as 500 individuals in recent months, probably for sale to pet shops in Las Vegas; this, predation on eggs by an introduced snail (*Melanoides tuberculata*), competition from other introduced fishes, or a combination of these factors could explain the apparent population decline of *Hypostomus* he felt had occurred. On 25 June 1981 a reexamination of the spring pond using a face mask and a light to observe the undercut banks demonstrated that *Hypostomus* continues to exist in relatively high density in Indian Spring. Individuals of all sizes were seen hiding in or around almost every available hole, tree root, or rock.

---

[1] Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33431.

[2] Department of Biology, University of Nevada, Las Vegas, Nevada 89154

Suckermouth catfish have been recorded as established in Texas (Barron 1964, Hubbs et al. 1978) and Florida (Courtenay and Robins 1973, Courtenay 1979b, 1980). The specimen collected at Indian Spring is morphologically distinct from those collected in Texas and Florida and represents a third species of *Hypostomus* established in the U.S.

Deacon (pers. comm. to D. A. Hensley) also recorded the green swordtail (*Xiphophorus helleri*) from Indian Spring in 1975. Although we found no green swordtails at Indian Spring on 18 October 1980, a yellow to pale orange hybrid swordtail (probably *X. helleri* x *X. maculatus*) was found to be the dominant fish in number of individuals. Guppies (*Poecilia reticulata*) were also abundant and several large common carp (*Cyprinus carpio*) were seen but not collected. The only other species present was the mosquitofish (*Gambusia affinis*).

Blue Point Spring is in the Lake Mead National Recreational Area above the Overton Arm of Lake Mead, approximately 68 km northeast of Las Vegas. Deacon et al. (1964) recorded guppies, shortfin mollies (*Poecilia mexicana*), and the southern platyfish (*Xiphophorus maculatus*) from Blue Point Spring. In a collection made 18 October 1980, no guppies or southern platyfish were found; however, shortfin mollies, convict cichlids, and a single spotted tilapia with damaged pelvic fins were captured. Deacon et al. (1964) also reported a transplant, the sailfin molly (*Poecilia latipinna*), from Blue Point Spring; we did not collect this species there and it is assumed that the population died out.

Rogers Spring is located 2 km southwest of Blue Point Spring in the Lake Mead National Recreational Area. Deacon et al. (1964) reported convict cichlids, goldfish (*Carassius auratus*) and transplanted sailfin mollies, golden shiners (*Notemigonus crysoleucas*), and mosquitofish from Rogers Spring. Hubbs and Deacon (1964) reported convict cichlids, shortfin mollies, transplanted sailfin mollies, and the banded cichlid (*Cichlasoma severum*) from this spring. An attempt to remove the introduced fishes was made in December 1963. We seined Rogers Spring on 18 October 1980. The dominant fish (in numbers and biomass) was the spotted tilapia (*Tilapia mariae*). Shortfin mollies were very abundant, convict cichlids were rare, and two guppies were collected. Underwater observations made prior to the seine hauls correlated well with the population densities revealed by seining. No banded cichlids, sailfin mollies, golden shiners, or mosquitofish were seen or collected, and they are considered as no longer extant in Rogers Spring.

Of particular interest were the underwater observations on spotted tilapia prior to seining activities. Most of the tilapias, even large individuals (above 100 mm SL), displayed the banded juvenile pattern as illustrated by Thys van den Audenaerde (1966). Only a relatively few large individuals showed the typical adult pattern of spots on their sides (Fig. 1). Moreover, it was later noted, following seining, that most of the tilapias displaying the juvenile color pattern were missing parts or most of their pelvic fins (Fig. 2) and that other fins (particularly the soft dorsal and upper half of the caudal) often showed damage. The only fish in Rogers Spring capable of inflicting such damage were the adults with the typical adult color pattern; none of those had damaged fins.

At no time have population densities of *Tilapia mariae* in Florida been observed to be approaching those seen in Rogers Spring. It is probable that the trophic and spatial carrying capacities of Rogers Spring for spotted tilapia have been reached and that this behavioral hierarchy, led by a few highly aggressive individuals, has developed to control further overpopulation.

LINCOLN COUNTY

Deacon et al. (1964) did not find any exotic fishes at either Crystal Spring or Ash Springs in the Pahranagat Valley, some 145 km north-northwest of Rogers Spring during collecting trips on 2 February and 9 March 1963. They did find an introduced population of mosquitofish at Ash Springs that was reported earlier by Miller and Hubbs (1960). During a collecting trip on 3 June 1964,

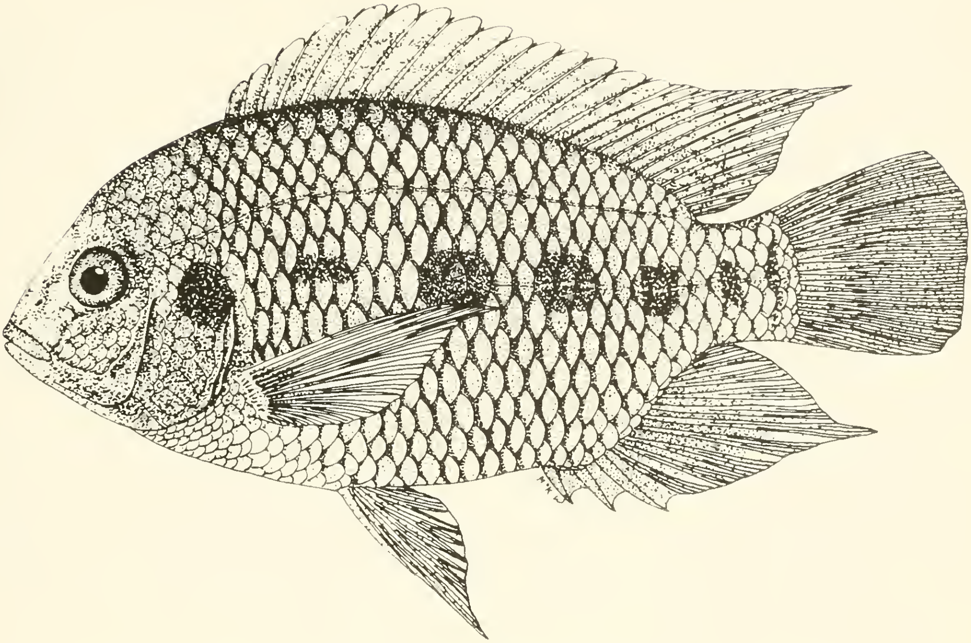


Fig. 1. An adult spotted tilapia, 205 mm standard length. Drawing by Francis McKittrick Watkins.

convict cichlids, shortfin mollies, and transplanted sailfin mollies were discovered in Ash Springs (Hubbs and Deacon 1964). The probable source of these introduced fishes was suggested as Rogers Spring because all three species were known to exist there. The same three non-native fishes subsequently spread from Ash Springs to Crystal Spring, 8 km to the north-northwest.

On 17 October 1980, surface and underwater observations, as well as seine collections, made in the outflow of Ash Springs showed convict cichlids to be dominant in biomass, followed by shortfin mollies that were dominant in numbers of individuals. Transplanted mosquitofish were common and no sailfin mollies were seen or collected. Introduced fishes were somewhat uncommon in a pool occupied by 35–40 individuals of the Pahranagat roundtail chub (*Gila robusta jordani*).

NYE COUNTY

Goldfish, *Carassius auratus*, were reported by Deacon et al. (1964) and by Deacon (1979) in Pahrump Valley at Manse Ranch Spring. Manse Ranch Spring dried up for a short time in the summer of 1975 (Soltz and Naiman 1978), thus eliminating the goldfish. About 10 km to the north of Manse Ranch Spring is the site of Pahrump Spring, originally the largest spring in Pahrump Valley. Pahrump Spring failed in the late 1950s because of excess pumping of groundwater for irrigation. During the late 1970s the surrounding area was subjected to a land development plan that included construction of a golf course and park area. The ponds and small stream associated with this development use groundwater from the vicinity of the former spring source. Examination of the main pond in Cottonwood Park by the Nevada Department of Wildlife on 4 March 1980 and by one of us (Deacon) on 16 July 1981 revealed the presence of large numbers of goldfish and mosquitofish and relatively small numbers of the redbelly tilapia, *Tilapia zilli*. The specimens of redbelly tilapia collected were all small, but one pair of larger fish (to ca 250 mm) was seen in the water in July, apparently guarding nests or young. The manager reported that large numbers of *Tilapia* died last winter when the water temperature reached 58 F (14 C). This species has maintained itself through at least two

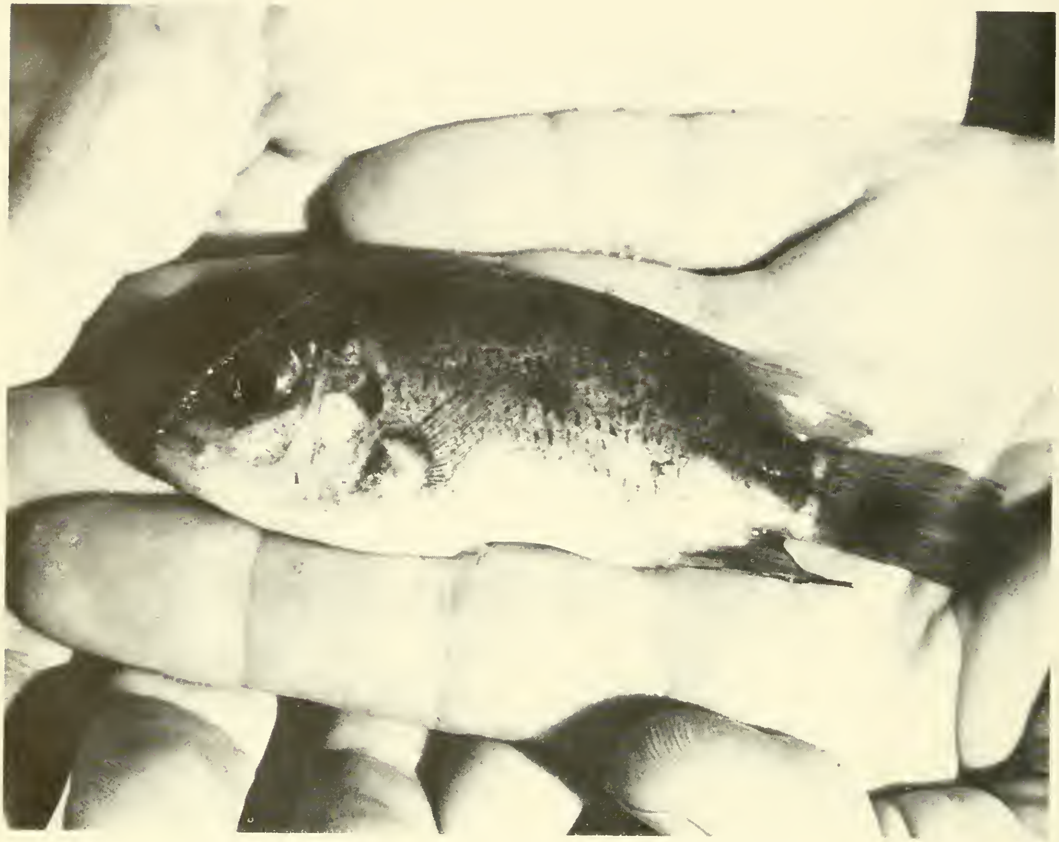


Fig. 2. A spotted tilapia, 73.5 mm SL, from Blue Point Spring. Note damaged pelvic fins.

winters and has reproduced during the summers of 1980 and 1981. A small population is able to exist through the winter apparently because the inflowing water maintains a temperature of about 70 F (21 C).

DISCUSSION

Courtenay et al. (1974) termed the promiscuous introduction of exotic fishes to new environments as biological pollution. Unlike chemical or thermal pollutants, biological additives have the ability to reproduce and expand their ranges. Moreover, many exotic fishes may appear to be trophic specialists in their native range but prove to be passive generalists (Birkeland and Neudecker 1981) in new environments where most or all of the biological constraints of the native range are absent (Courtenay and Hensley 1980). Such trophic adaptation, coupled frequently with equally adaptable behavioral traits, permits the exotic species to disrupt habitats and niches (*sensu lato*) in new environments.

The introduction of any non-native fish will result in alterations in the host ecosystem. Such alterations may range from minor, almost unnoticeable changes in native fish populations to the extinction of one or more native species (Courtenay 1979a, Courtenay and Hensley 1980). In Florida, for example, comparatively small ornamental fishes, cichlids in particular, are able to successfully invade and become dominant in waters that contain larger native piscivores such as largemouth bass (*Micropterus salmoides*) and Florida gar (*Lepisosteus platyrhincus*). Invasion and domination by nonnative fishes in many parts of the desert southwest is facilitated by the absence of piscivores and the presence of small endemic fishes that have had no previous experience with trophic passive generalists or piscivores. Therefore, a fish that feeds on phytoplankton or detritus in its native range and either becomes a predator of smaller fishes or feeds on algae in the new environment is a clear threat to many native fishes in the southwestern U.S.

It is obvious that there have been several changes in the introduced fish fauna in southern Nevada since 1963. Species compositions have changed. The green swordtail population in Indian Spring is gone and has been replaced with a hybrid of *Xiphophorus*; a population of a suckermouth catfish remains extant there. Guppies, southern platyfish, and sailfin mollies appear to be absent in Blue Point Spring, and at least one spotted tilapia was released, probably recently, before our collections there. Sailfin mollies, mosquitofish, and the banded cichlid are absent in Rogers Spring, the latter probably due to the eradication effort in 1963; convict cichlids are now rare, but guppies and spotted tilapia (the latter now dominant) have been added. Sailfin mollies appear to be absent from the outflow of Ash Springs in the Pahranagat Valley, whereas convict cichlids and shortfin mollies are dominant, 17 years after their introduction.

Frequent and closer monitoring of introduced fish populations, particularly in areas that are potential or recognized release sites for unwanted pet fishes in southern Nevada and other areas in the desert southwest, is needed. These "pockets" of introduced fishes serve as potential and probable sources for future introductions elsewhere as apparently occurred with the transfer of convict cichlids and shortfin mollies from Rogers Spring to Ash Springs in 1963. A further indication of the constant or continuing nature of this problem is a verbal report from Mr. Charles Orr, a Las Vegas member of the American Cichlid Association, that he saw and identified several specimens of the "marmalade" form of *Pseudotropheus zebra* when he visited Rogers Spring in July 1981.

Although the disappearance of some introduced fishes in southern Nevada in recent years may be of some interest, it is far more important that studies be initiated to define the impacts of introduced species on native fishes. Species interactions between nonnative and native fishes have been suggested as reasons for declines in populations of native fishes (Deacon et al. 1964, Hubbs and Deacon 1964, Courtenay and Hensley 1980), but to date the exact mechanisms for these declines have not been examined. The "cause and effect" for such declines is suggested strongly but requires in situ observations and evaluations.

Finding an established population of spotted tilapia in southern Nevada is particularly disturbing. Although this fish is omnivorous, it shows a preference for green algae in Florida and in its native range has been described as "une forme intermédiaire entre les *Tilapia* herbivores et les espèces microphages" (Thys van den Audenaerde 1966). The bottom of Rogers Spring was devoid of green algae, doubtlessly due to grazing by spotted tilapia. A trophic preference of this type, coupled with omnivory, could prove disastrous to several endemic species and subspecies of southwestern fishes if this western African cichlid were moved elsewhere. We therefore recommend its immediate eradication. Much the same result could be expected by future introductions of other tilapias (*sensu lato*) or such seemingly harmless fishes as *Hypostomus* spp. Also, the potential introduction of fish parasites via exotic fish vectors exists (Lachner et al. 1970, Courtenay and Robins 1975, Courtenay 1979a) and has been suggested to have occurred in southern Nevada (Deacon 1979) and elsewhere (Hoffman 1970, Bauer and Hoffman 1976).

Fish introductions pose as great a threat to the continued existence of the depauperate fish fauna in southern Nevada and adjoining states as does water withdrawal for agricultural, domestic, military, and industrial uses or other habitat modifications.

ACKNOWLEDGMENTS

We thank Paul Greger and Thom Hardy for assistance in the field and James A. McCann, Robert R. Miller, and Jeffrey N. Taylor for their helpful comments on the manuscript. This study was supported by Contract 14-16-0009-78-021, Cooperative Agreement 14-16-0009-80-952, and an Intergovernmental Personnel Act Assignment from the Department of the Interior, U.S. Fish and Wildlife Service, and by sabbatical funding from Florida Atlantic University.

LITERATURE CITED

BARRON, J. C. 1964. Reproduction and apparent overwinter survival of suckermouth armored catfish, *Plecostomus* sp., in the headwaters of the San Antonio River. Texas J. Sci. 16:449–450.

BAUER, O. N., AND G. L. HOFFMAN. 1976. Helminth range extension by translocation of fish. Pages 163–172 *in* L. A. Page, ed., Wildlife diseases. Plenum Publ. Corp., New York.

BIRKELAND, C., AND S. NEUDECKER. 1981. Foraging behavior in two Caribbean chaetodontids: *Chaetodon capistratus* and *C. aculeatus*. Copeia 1981 (1):169–178.

COURTENAY, W. R., JR. 1979a. The introduction of exotic organisms. Pages 237–252 *in* H. P. Brokaw, ed., Wildlife and America. Government Printing Office, Washington.

———. 1979b. Biological impacts of introduced species and management policy in Florida. Pages 237–257 *in* R. Mann, ed., Exotic species in mariculture. MIT Press, Cambridge, Massachusetts.

———. 1980. Exotic fish: environmental roulette. Water Spectrum 12(4):10–17.

COURTENAY, W. R., JR., AND D. A. HENSLEY. 1979. Range expansion in southern Florida of the introduced spotted tilapia. Environ. Conserv. 6(2):149–151.

———. 1980. Special problems associated with monitoring exotic species. Pages 281–307 *in* C. H. Hocutt and J. R. Stauffer, Jr., eds., Biological monitoring of fish. Lexington Books, Lexington, Massachusetts.

COURTENAY, W. R., JR., AND C. R. ROBINS. 1973. Exotic aquatic organisms in Florida with emphasis on fishes: a review and recommendations. Trans. Amer. Fish. Soc. 102(1):1–12.

———. 1975. Exotic organisms: an unsolved, complex problem. BioScience 25(5):306–313.

COURTENAY, W. R., JR., H. F. SAHLMAN, W. W. MILEY II, AND D. J. HERREMA. 1974. Exotic fishes in fresh and brackish waters of Florida. Biol. Conserv. 6(4):292–302.

DEACON, J. E. 1979. Endangered and threatened fishes of the west. Great Basin Nat. Mem. No. 3:41–64.

DEACON, J. E., C. HUBBS, AND B. J. ZAHURANEC. 1964. Some effects of introduced fishes on the native fish fauna of southern Nevada. Copeia 1964 (2):384–388.

HARDY, T. 1980. The Inter-Basin area report. Proc. Desert Fish. Coun. 11:5–21.

HOFFMAN, G. L. 1970. Intercontinental and transcontinental dissemination and transfaunation of fish parasites with emphasis on whirling disease (*Myxosoma cerebralis*). Pages 69–81 *in* S. F. Snieszko, ed., A symposium on diseases of fishes and shellfishes. Amer. Fish. Soc. Spec. Publ. 5.

HOGG, R. G. 1974. Environmental hazards posed by exotic fish species newly established in Florida. Environ. Conserv. 1(3):176.

———. 1976. Established exotic cichlid fishes in Dade County, Florida. Florida Sci. 39(2):97–103.

HUBBS, C., AND H. J. BRODERICK. 1963. Current abundance of *Gambusia gaigei*, an endangered fish species. Southwest Nat. 8:46–48.

HUBBS, C., AND J. E. DEACON. 1965. Additional introductions of tropical fishes into southern Nevada. Southwest Nat. 9(4):249–251.

HUBBS, C., T. LUCIER, G. P. GARRETT, R. J. EDWARDS, S. M. DEAN, E. MARSH, AND D. BELK. 1978. Survival and abundance of introduced fishes near San Antonio. Texas J. Sci. 30(4):369–376.

HUBBS, C. L., R. R. MILLER, AND L. C. HUBBS. 1974. Hydrographic history and relict fishes of the north central Great Basin. California Acad. Sci. Mem. 7:1–259.

LACHNER, E. A., C. R. ROBINS, AND W. R. COURTENAY, JR. 1970. Exotic fishes and other aquatic organisms introduced into North America. Smithson. Stud. Zool. 59:1–29.

LA RIVERS, I. 1962. Fishes and fisheries of Nevada. Nevada St. Fish and Game Comm. 782 pp.

MILLER, R. R. 1961. Man and the changing fish fauna of the American southwest. Pap. Mich. Acad. Sci., Arts. and Lett. 46:365–404.

MILLER, R. R., AND J. R. ALCORN. 1946. The introduced fishes of Nevada, with a history of their introduction. Trans. Amer. Fish. Soc. 73:173–193.

MILLER, R. R., AND C. L. HUBBS. 1960. The spiny-rayed cyprinid fishes (Plagopterini) of the Colorado River system. Misc. Publ. Mus. Zool. Univ. Michigan 115:1–39.

MINCKLEY, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Dept., Phoenix. 293 pp.

MINCKLEY, W. L., AND J. E. DEACON. 1968. Southwestern fishes and the enigma of "endangered species." Science 159:1424–1432.

SOLTZ, D. L., AND R. J. NAIMAN. 1978. The natural history of native fishes in the Death Valley system. Natural History Museum of Los Angeles County, Science Series 30:1–76.

THYS VAN DEN AUDENAERDE, D. F. E. 1966. Les tilapia (Pisces, Cichlidae) du sud-Cameroun et du Gabon; étude systématique. Ann. Mus. Roy. Afr. Cent., ser. 8, Zool. 153:1–98.

WILSON, B. L., J. E. DEACON, AND W. G. BRADLEY. 1966. Parasitism in the fishes of the Moapa River, Clark County, Nevada. Trans. California-Nevada Sec. Wildl. Soc. pp. 12–23.

A NEW SPECIES OF *PENSTEMON* (SCROPHULARIACEAE) FROM THE UINTA BASIN OF UTAH AND COLORADO

John Larry England[1]

Abstract.— Named as a new species is *Penstemon albifluvis* J. L. England. The species is known from the Uinta Basin of Utah and Colorado.

The Uinta Basin of Utah and Colorado harbors numerous endemic species of plants, with many of these restricted to the Green River Formation. It is not surprising that this habitat should give rise to yet another narrowly restricted species. The author, while employed by the Bureau of Land Management, encountered a novel *Penstemon* growing on oil shale ledges of the Green River Formation immediately adjacent to the White River. Subsequent examination revealed this botanical novelty to be distinct from any described taxon. Hence, it is described herein.

Penstemon albifluvis England, sp. nov.

Ab *Penstemon scariosus* et *P. strictus* in calycibus et corollis brevioribus et foliis radicalibus paucis vel nullis et pubis antheris brevioribus differt.

Perennial herb; stems ascending to erect, (1) 1.5–4.5 (5) dm tall, (1) 5–20 clustered on a frequently branched caudex, surmounting a taproot; herbage glabrous; leaves entire or with crisped margins (2) 4–10 (12) cm long, 4–6 (11) mm wide, lacking basal leaves or these poorly developed, lower cauline leaves narrowly oblanceolate, petiolate, the upper cauline ones mostly linear to narrowly lanceolate, sessile, often crisped margined; thyrse secund, of 3–10 verticillasters, the upper leafy bracts much reduced, the cymes (1) 2- to 4-flowered, the axis, peduncles, and pedicels glandular-pubescent; sepals 4–6 (7) mm long, lanceolate, acute, glandular-pubescent, the margins narrowly scarious; corolla (18) 20–22 (24) mm long, gradually and broadly ventricose ampliate, the throat 6–7 mm broad, the tube 14–15 mm long, bilabiate, the upper lip projecting, arched, 7–8 mm long, the lobes of the lower lip spreading, pale lavendar, the lobes sometimes light blue, sparsely glandular-pubescent externally, the palate with two ridges 1 mm high on either side of the staminode, glabrous; staminode 9–10 mm long, ending ca 1 mm short of the groove in the palate, straight apically, sparsely orange bearded, with hairs 0.2–.3 mm long, gradually enlarged apically, from 0.3–0.7 mm broad; fertile stamens reaching the orifice, the anther sacs 3–5 mm long, 0.5 mm broad, pubescent, the hairs white, 0.5 mm long or less, dehiscing the full length, black; capsule 8–11 mm long, broadly ovoid, acuminate; seeds ca 2 mm long.

Type.— USA. Utah: Uintah Co., North bank of White River, ca one mile upstream from the Ignatio bridge, 2.5 miles airline distance south of Bonanza, T10S, R24E, S1, elevation 4975 ft, on raw shale slopes of the Evacuation Creek Member of the Green River Formation, associated with *Eriogonum ephedroides, Cirsium barnebyi, Machaeranthera grindelioides, Oryzopsis hymenoides,* and *Forsellesia meionandra*, 9 June 1980, J. L. England 2046 (Holotype BRY; Isotypes to be distributed).

The White River penstemon grows on raw shales with little soil development with *Eriogonum, Cirsium,* and *Forsellesia* in the desert saltbrush-sagebrush zone. It is endemic to east central Uintah County, Utah, and adjacent Rio Blanco County, Colorado. The plants flower from late May through June.

---

[1] U.S. Fish and Wildlife Service, 125 South State Street, Salt Lake City, Utah 84138.

TABLE 1. Characteristics of *Penstemon albifluvis* and its relatives.

	P. albifluvis	*P. scarious*	*P. strictus*
Calyx length	4-6(7) mm	(4) 6-9 mm	3-8 (10) mm
Corolla length	(18) 20-22 (24) mm	(20) 24-30 mm	(20) 24-30 mm
Basal leaves	lacking or poorly developed	well developed	well developed
Anther pubescence	hairs less than width of anthers	many hairs longer than width of anthers	many hairs longer than length of anthers
Habitat	On poorly developed soils of Green River Formation on very xeric sites; 1500-1700 m	higher elevations to deeper well-developed soils at lower elevations on variable geologic substrates 2000-3000 m	higher elevations to deeper well-developed soils at lower elevations on variable geologic substrates 1800-3200 m

Penstemon albifluvis is a member of the section Glabri (Pennell 1920) and has strong affinities to the pubescent anthered members of that section, most notably *Penstemon scariosus* and *P. strictus*. The characteristics of the White River penstemon and its relatives are compared in Table 1.

LITERATURE CITED

PENNELL, F. W. 1920. Scrophulariaceae of the Central Rocky Mountain States. Contr. U.S. National Herb. 20: 313-381.

PHALACROPSIS DISPAR (COLEOPTERA: PHALACRIDAE), AN ELEMENT IN THE NATURAL CONTROL OF NATIVE PINE STEM RUST FUNGI IN THE WESTERN UNITED STATES[1]

David L. Nelson[2]

Abstract.— Larvae of the phalacrid beetle *Phalacropsis dispar* (LeConte) consumed aeciospores and the underlying sporogenous mycelium, thereby destroying the aecia of all native western pine stem rust fungi studied. Aecia of the introduced white pine blister rust fungus (*Cronartium ribicola*) were not found to be infested by the beetle. A close, if not obligate, biosis of the beetle apparently exists with the native rust fungi, and their geographic distributions closely coincide. Laboratory tests and field observations indicate that the beetle completes its life cycle in 30 to 40 days and apparently overwinters as an adult. Quantitative data on aeciospore inoculum destruction were beyond the means of this study; however, observations over a 12-year period evidenced widespread and extensive destruction of aeciospores. The beetle may be an effective element in the natural control of native pine stem rust fungi. Natural control by secondary organisms could significantly reduce the selective pressure for high host resistance in a naturally evolving host-parasite population.

Direct control of pine stem rust disease problems through application of chemicals and eradication of alternate hosts is usually expensive and of questionable effectiveness (Toko et al. 1967, Leaphart and Wicker 1968, Peterson and Jewel 1968, Carlson 1978). Various silvicultural methods (Peterson 1966, Van Arsdel 1961, Nighswander and Patton 1965, Krebill 1968) and selection for host resistance appear to be the most acceptable means to immediate and long-term control (Hanover 1966, Bingham et al. 1971, Hiratsuka and Powell 1976). Research on pine stem rust in the western United States has concentrated on the exotic white pine blister rust (*Cronartium ribicola* Fisch. in Rabenh.). The native rusts are currently not considered important enough to justify more than limited study. Natural control other than host resistance may be an important factor in allowing this option. Answers for low-cost control of conifer rust diseases considered important could come from study of the natural control of native rust fungi. This may be especially true in the less extensively managed forests of western North America.

Host tissue affected by pine stem rusts and the fruiting bodies of the aecial state of the rust fungi provide an attractive habitat and food source for many other organisms. These are mainly fungi (Mielke 1933, Wollenweber 1934, Powell 1971a,b,c, Byler et al. 1972b, Williams 1972, Kuhlman and Miller 1976, Kuhlman et al. 1976, Hiratsuka et al. 1979, Tsuneda and Hiratsuka 1979, 1980, Tsuneda et al. 1980, Kuhlman 1981a,b), insects (Snell 1919, Myren 1964, Coulson and Franklin 1970, Powell 1971d,e, Furniss et al. 1972, Powell et al. 1972, Kuhlman 1981b), and, to a lesser extent, rodents (Mielke 1935, Powell 1974) and mollusks (Hunt 1978). They may play a more important role than is recognized in the selection and limitation of these rust fungi through reduction of aecial inoculum.

This study provides information on the identity, life history, and distribution of an aeciospore-consuming phalacrid beetle and suggests the possible importance of its destruction of aecia and the activity of other reported secondary organisms in the natural control of some western native pine stem rust fungi.

Review

Many insects and other arthropods are associated with pine stem and cone rusts in North America. Of special interest here are those that attack the rust fungi directly, are dependent upon them, consume large amounts of aeciospores, and consume or damage sporogenous mycelium.

---

[1] This article was written and prepared by a United States government employee on official time, and it is therefore in the public domain.

[2] Intermountain Forest and Range Experiment Station, Shrub Sciences Laboratory, Provo, Utah 84601. The initial observations for this study were made while the author was a student at the University of California, Berkeley.

Hubert (1923) described the activity of *Epuraea ovata* Horn (Coleoptera: Nitidulidae) larvae as consuming the entire aeciospore mass and underlying stromatic mycelium of the western gall rust fungus, *Endocronartium harknessii* (*Peridermium harknessii*). Powell (1971d) reviewed insects associated with pine stem rusts and listed 160 species of arthropods he found on *Cronartium comandrae* blister rust cankers on *Pinus contorta* Dougl. Powell et al. (1972) listed those found associated with *E. harknessii, C. comandrae, C. coleosporioides*, and *C. comptoniae* Arth. Using Graves's and Benick's system of classification, Powell (1971d) classed *Epuraea obliquus* Hatch, *Paracacoxenus gluttatus* Haryd & Wheeler (Diptera: Drosophilidae), and a mite, *Diapterobates principalis* Berlese (Acarina: Ceratozetidae), as apparent true mycetobionts completely dependent on the aecia of *C. comandrae* for food. *Epuraea obliquus* was also found associated with *C. coleosporioides, Endocronartium harknessii*, and *C. comptoniae* (Powell et al. 1972). Species of 12 genera of the insect orders Homoptera, Coleoptera, Lepidoptera, and Diptera associated with comandra blister rust (*C. comandrae*) cankers were considered to be apparent facultative mycetophiles. Several species of the mycetophilous type, especially the cone moth *Dioryctria* spp. (Lepidoptera: Pyralidae), extensively damaged areas of the aecial and spermogonial zone by burrowing in infected phloem tissue. Similar behavior of this moth has been observed on *C. fusiforme* Hedgc. & Hunt (Coulson and Franklin 1970), *C. strobilinum* (Arth.) Peterson (Merkel 1958), *C. comptoniae* (Anderson and French 1964), *E. harknessii* (Byler et al. 1972a), and *C. coleosporioides* (Powell 1971d). Powell (1971d) regarded most of the 38 species of Hymenoptera he observed as parasitic on Lepidoptera, Diptera, and Coleoptera that inhabited the rust cankers. Furniss et al. (1972), examining cankers of white pine blister rust in northern Idaho, found some of the species described by Powell (1971d) and Powell et al. (1972), but the number and diversity of species were considerably less. The only apparent true mycetobiont type found by Furniss et al. was *Paracacoxenus gluttatus*.

The extent to which pine stem rusts are damaged by these insects has received little study, and the impact of insect attacks on reduction of aeciospore inoculum and on subsequent infection of pine has received even less. Over a seven-year period, between 32 and 57 percent of the *C. comandrae* cankers received obvious annual damage on 23 locations, according to Powell (1971b). From 60 to 80 percent of the cankers were damaged yearly over this period. Insects infested up to 49 percent of recently dead or damaged galls of *E. harknessii* on *Pinus radiata* D. Don on one plot in California (Byler et al. 1972a). Nearly 45 percent of the *E. harknessii* galls studied by Wong (1972) in Manitoba and Saskatchewan over a four-year period were mined by larvae of *Dioryctria banksiella* Mutuura, Munroe, and Ross, but Wong gave no information on damage to the rust fungus. Attacks by some insects that consume aeciospores can be severe. Studies in southwestern Alberta (Powell 1971d) indicated a yearly 10 percent reduction in aeciospore production, with some years having a much higher percentage. *Epuraea obliquus* occurred on as many as 80 percent of the sporulating cankers on a single location, with at least 50 percent being attacked over a five-year period. Dipterous and lepidopterous larvae were observed on over 25 percent of sporulating cankers in certain locations. The activity of *Dioryctria* sp., *E. lengi* Parsons, unknown dipterous larvae, and other insects apparently was of little importance in reducing aeciospore inoculum of southern fusiform rust in North Carolina according to Kuhlman (1981b).

METHODS

During other research on native western conifer rusts, a beetle was frequently observed in the aecia of pine stem rust fungi. The beetle's distribution and activity were studied on annual field trips from 1963 through 1975. Observations were made in coastal California from Fort Bragg south to the San Francisco Bay area and the Sierra Nevada, western Nevada from Lake Tahoe south to the Spring Mountains north of Las Vegas, northern Arizona south to Prescott, most of Utah, extreme western Wyoming,

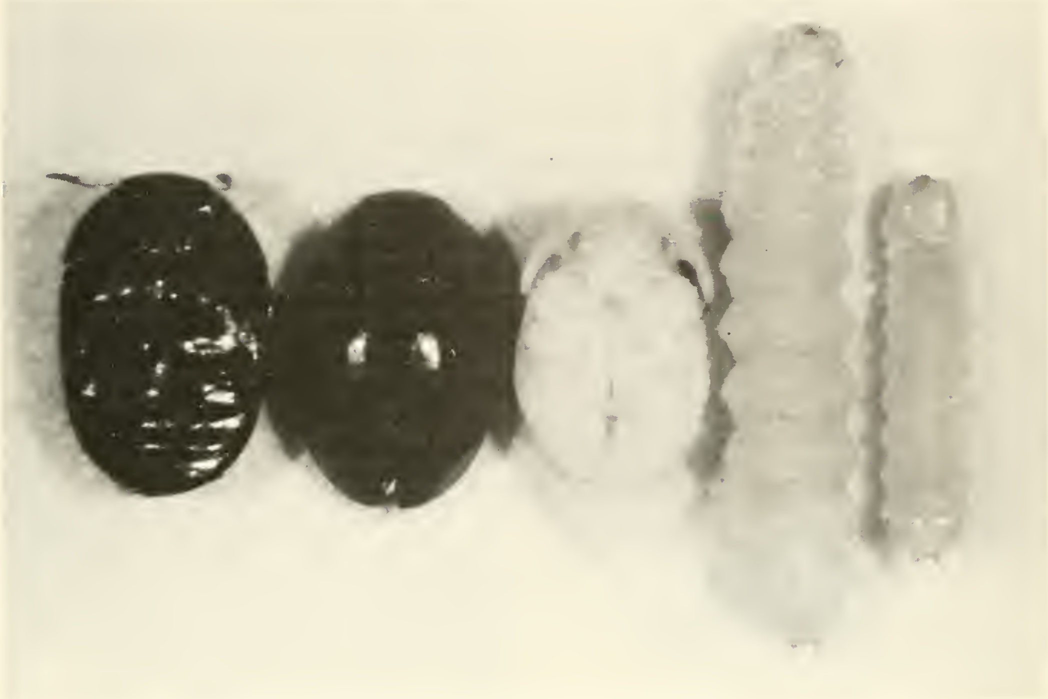


Fig. 1. Adult, pupal, and larval stages of *Phalacropsis dispar*, enlarged 14 times.

southern Idaho from the Salmon River south, and east central Oregon.

Because of the uncertain taxonomic status of some of the rust fungi involved and because the study is concerned with the aecial state, the imperfect or peridermium name of some of the rust fungi will be used for clarity throughout the remainder of the paper.

To obtain information on beetle life history, rust-infected stem sections that were also beetle infested were collected for laboratory study. Infested rust samples were placed in one-liter glass beakers for observation. Drying of specimens was slowed by covering beaker tops with a plastic film punctured in several places to allow air exchange. Cheesecloth was placed over the film to prevent escape of insects. Thus assembled, the specimens were held in the laboratory at normal room temperature, approximately 21 C. Both natural and fluorescent light was received during the day. Observations on development were made daily when possible. Dates when larvae matured, pupation began, and adult beetles emerged were recorded.

Three locations were selected for annual field observation of beetle activity and rust development: (1) Bucks Lake, Plumas National Forest, Plumas County, California; (2) Lee Vining Creek, Toiyabe National Forest, Inyo County, California; and (3) Red Canyon, Dixie National Forest, Garfield County, Utah. At location one, western gall rust, caused by *Peridermium harknessii* (*Endocronartium harknessii*), was present on *Pinus ponderosa* Laws.; at location two, limb rust and stalactiform canker rust (both caused by *Peridermium stalactiforme* [Peterson 1968], an imperfect state of *Cronartium coleosporioides*), were present on *Pinus jeffreyi* Grev. & Balf. and *P. contorta*, respectively; and at location three, Powell limb rust (Peterson 1968), caused by *Peridermium filamentosum*, was present on *Pinus ponderosa*. Observations were made at location one from 1963 through 1975 and at locations two and three from 1967 through 1975. These locations were visited one to three or more times each year during the aecial sporulation period.

Results

Habitat and Identification

Numerous small, white-to-grayish beetle larvae (Fig. 1) were frequently found in the

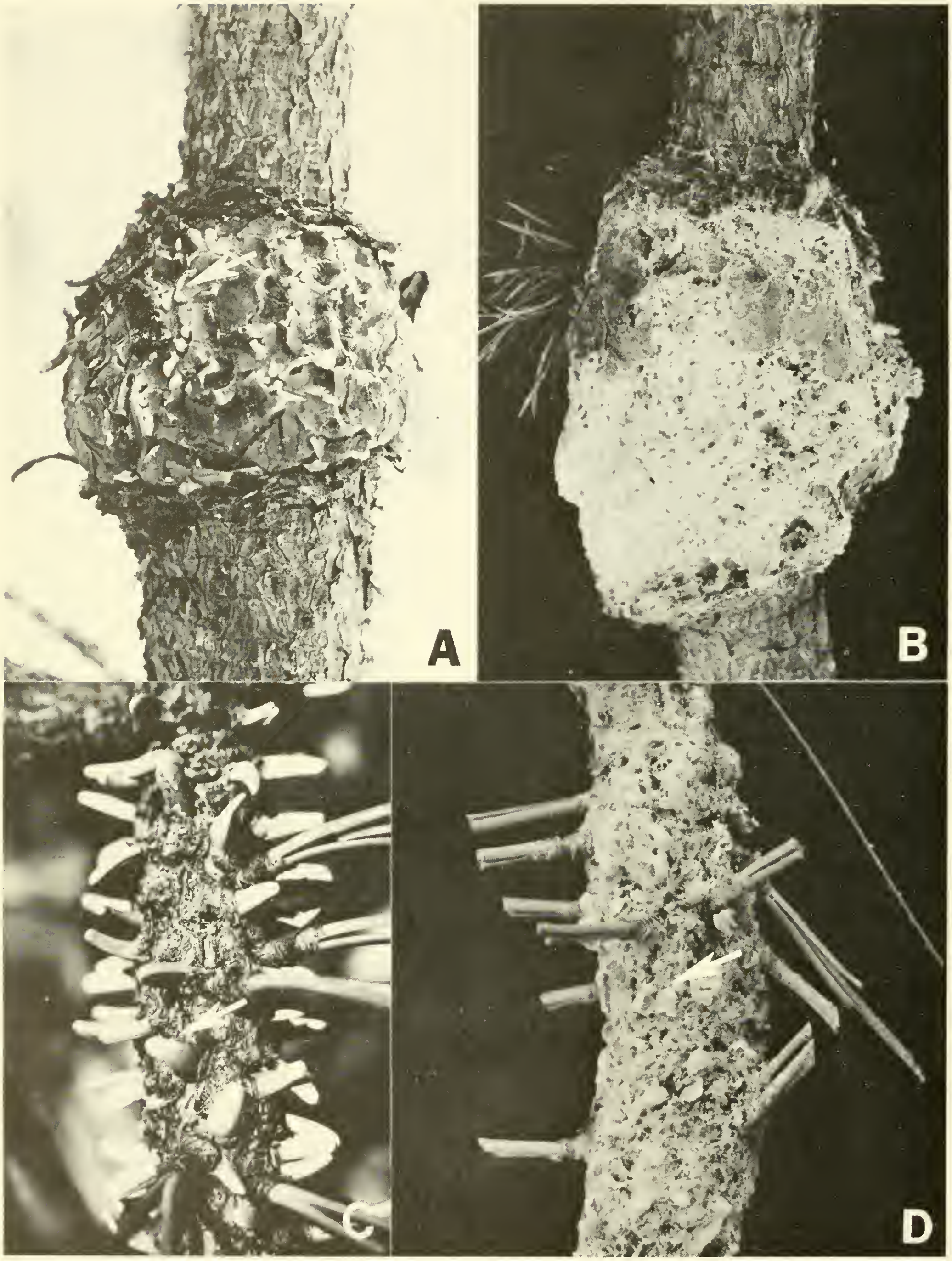


Fig. 2. Beetle-damaged pine stem rusts (note weblike fecal debris over surface of stems): western gall rust (A) unopened, uninfested aecia (arrow) one-half actual size; (B) insect-damaged aecia; limb rust (C) unopened, uninfested aecia (arrow) actual size; (D) insect-damaged aecia (arrow points to unconsumed peridial fragments).

aecial spore masses (Fig. 2A–D) of the various pine stem rust fungi observed. Their voracious consumption of aeciospores and of the underlying sporogenous mycelium effectively reduced aecia (Fig. 2A, C) to a mass of fecal debris within several weeks' time (Fig. 2B, D). Microscopic examination of young larvae revealed that the gut and intestinal tract were full of aeciospores. Masses of spores were discharged in strings of fecal pellets. Several germination tests of aeciospores from fecal pellets failed to show any viability. Unconsumed spores in the same collections germinated. Spores of secondary fungi (such as *Penicillium*, which commonly invade aecial masses [Byler et al. 1972a]) were also consumed by the larvae. The peridium of aecia was not consumed.

Beetle specimens reared in the laboratory from larval-infested western gall and limb rust samples were used for identification. Larvae pupated and developed into shiny chestnut brown beetles about 3 mm in length (Fig. 1). They were identified as *Phalacropsis dispar* (LeConte) by Dr. Carl T. Parsons, who confirmed his identification by comparing specimens with the type specimen at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Phalacropsis is a monotypic genus described by T. L. Casey (1889–1890). The type specimen was collected in 1878 by E. A. Schwarz on a geological survey at 9400 ft on Veta Pass, Colorado, and described by T. L. Le Conte (1879). No host plant was mentioned. *Phalacropsis dispar* apparently is rarely collected. A check of 20 insect museums throughout the United States revealed only six collections as follows: California Academy of Sciences, Golden Gate Park—two collections, both from the Sierra Nevada, one on *Pinus* sp., no host listed for the other specimen; Ohio State University—two collections, one from Yosemite National Park, California, the other from the Chiricahua Mountains of Arizona, no hosts were listed; and National Museum of Natural History—two collections, one from the Sitgreaves National Forest, Arizona, on *Pinus ponderosa* and the other from Pringle, South Dakota, on *Peridermium harknessii* aecia. Mountainous locations and hosts from which the specimens were collected indicate they all could be from pine stem rust aecia. Specimens of *Phalacropsis dispar* collected during this study have been deposited in the Museum of Comparative Zoology (Agassiz Museum), Harvard University, and the National Museum of Natural History Smithsonian Institution, Washington, D.C.

Distribution

The distribution of *P. dispar* observed in this study is indicated in Figure 3 and Table 1. With few exceptions, the beetle was found wherever pine stem rust fungi were examined closely during the aecial sporulation period. The most intensive study was made in Utah and in the Sierra Nevada of California, and the number of sites for the beetle in these areas (Fig. 3) is a reflection of this and is not necessarily an indication of abundance.

During a five-year study of western gall rust on pines in coastal areas of California, *P. dispar* was not encountered, nor was it listed by Byler et al. (1972a), who studied the same rust in these areas. In north coastal California near Fort Bragg, however, an unidentified larva of similar habit was abundant in aecia of *Peridermium harknessii* on *Pinus contorta*

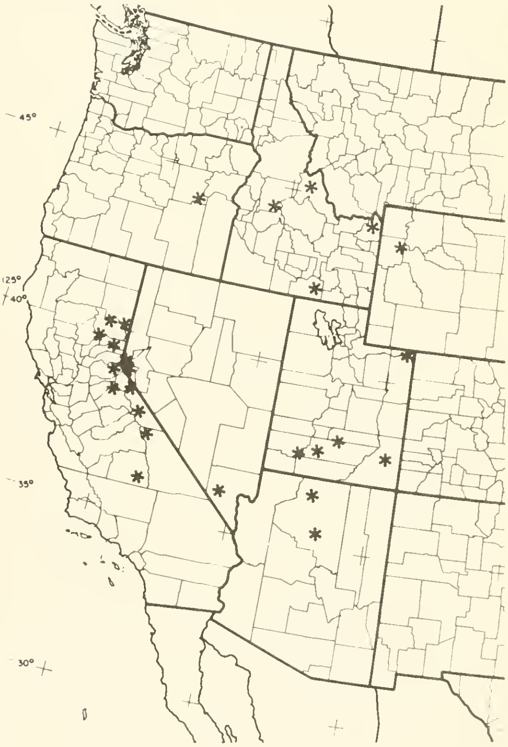


Fig. 3. Distribution of *Phalacropsis dispar* observed in this study on pine stem rust fungi in the western United States.

ssp. *bolanderi* (Parl.). Several attempts to rear adults failed. In the Sierra Nevada, *Phalacropsis dispar* was found on *Peridermium filamentosum* Inyo form (Peterson 1968), *P. stalactiforme* both forms, *P. harknessii*, *Cronartium occidentale*, and "Bethel" blister rust (Dixon 1978) (Table 1). *Cronartium comandrae* was not studied in this area. In the Bucks Lake area, *Phalacropsis dispar* was not found in aecia of the introduced *C. ribicola* on *Pinus lambertiana* (Dougl.). In this area, the *C. ribicola*-infected *P. lambertiana* occurred in several stands that were intermixed with *Peridermium harknessii*-infected *Pinus ponderosa* and *P. contorta*. The aecia of *Peridermium harknessii* on these pines were infested with *Phalacropsis dispar.* In the Spring Mountains of southern Nevada, *P. dispar* was found on the Coronado and Powell (Peterson 1968) forms of *Peridermium filamentosum* limb rust and was especially abundant on the albino form (Mielke and Peterson 1967) of western gall rust on *Pinus ponderosa*. In Arizona, *Phalacropsis dispar* was observed on the Coronado and Powell forms of *Peridermium filamentosum* limb rust on *Pinus ponderosa* on the Kaibab Plateau and in the San Francisco Mountains. In Utah, *Phalacropsis dispar* occurred on the Coronado and Powell forms of *Peridermium filamentosum* limb rust on *Pinus ponderosa* in the Abajo Mountains and on the Aquarius and Markagunt Plateaus in the southern end of the state. It also occurred on the Powell *Peridermium filamentosum* limb rust on *Pinus ponderosa* at the eastern end of the Uinta Mountains in northeastern Utah. It was not found on *C. comandrae*, *Peridermium harknessii*, and *P. stalactiforme* on *Pinus contorta* in the Wasatch Mountains of northern Utah. *Phalacropsis dispar* was found—although rarely—on *C. comandrae* on *Pinus contorta* on the Cassia Plateau of southern Idaho and on the northern end of the Wind River Range in western Wyoming. It occurred in *Peridermium harknessii* aecia on *Pinus contorta* in the Island Park area of eastern Idaho and on the same rust on both *P. contorta* and *P. ponderosa* in the Sawtooth Mountains in the south central part of the state. It was found

TABLE 1. The *Peridermium* species of pine stem rust fungi found in this study to be infested by *Phalacropsis dispar* in the western United States.

Peridermium rust	Pine host	Location
Cronartium coleosporioides Arth.		
Peridermium filamentosum Peck		
Coronado limb rust	*Pinus ponderosa*	Arizona, Nevada, Utah
Powell limb rust	*Pinus ponderosa*	Arizona, Nevada, Utah
Inyo limb rust	*Pinus jeffreyi*	California
Peridermium stalactiforme Arthur & Kern		
Stalactiforme limb rust	*Pinus jeffreyi*	California, Nevada
Stalactiforme canker rust	*Pinus contorta*	California, Oregon
	Pinus ponderosa	Idaho
Endocronartium harknessii (J. P. Moore) Y. Hiratsuka		
(*Peridermium harknessii* J. P. Moore)		
Western gall rust	*Pinus contorta*	California, Idaho, Oregon
	Pinus ponderosa	California, Idaho
Albino western gall rust	*Pinus ponderosa*	Nevada, Utah
Cronartium comandrae Peck		
Peridermium pyriforme Peck		
Comandra blister rust	*Pinus contorta*	Idaho, Wyoming
"Bethel" blister rust	*Pinus contorta*	California
Cronartium occidentale Hedg., Bethel, & Hunt		
Peridermium occidentale Hedg., Bethel, & Hunt		
Pinyon blister rust	*Pinus monophylla*	California

on a single canker of *Peridermium stalactiforme* on *Pinus ponderosa* in the Salmon River Mountains. In the Malheur National Forest of Oregon, *Phalacropsis dispar* was found on *Peridermium harknessii* and *P. stalactiforme* on *Pinus contorta*. In the central Idaho and Oregon areas mentioned, larvae and adults of an *Epuraea* sp. (another aeciospore-consuming beetle) were also present. From northern Utah northward, occurrence of *Phalacropsis dispar* was less frequent to rare and southward from this point it was increasingly abundant.

Life History Observations

Phalacropsis dispar was first noted in mid-May near Bucks Lake and in late May at Lee Vining and Red Canyon. Aecia of the associated rust fungi were just beginning to appear through the bark. On sunny days, adult beetles were seen on rusted limbs, crawling about and copulating. Egg-laying by the beetle was observed only in association with *Peridermium filamentosum* on *Pinus jeffreyi* in the Sierra Nevada of California. Single eggs were deposited at the exterior base of aecia. Larval activity began before full development of aecia and well in advance of peridial rupture. With the beginning of aeciospore release, larval activity had reached a peak. Beyond this stage, in the case of early sporulating rust fungi, adult beetles were not seen on rusted limbs; however, in the case of later sporulating Powell and Inyo forms of *Peridermium filamentosum*, adults were seen throughout July and August well after aecial maturity. After larval maturity, the insect disappeared from rusted limbs and galls and possibly pupated in the needle duff at the base of trees. Whether or not the insect overwinters in the pupal or adult stage in its natural environment was not studied.

In laboratory tests (Table 2), rusted stems were collected 10 to 15 days after adults were first seen. The first larvae began moving from aecia about 6 days after rust specimens were placed in glass beakers in the laboratory. Pupation began 4 to 7 days later on the floor of the beaker under masses of fecal debris, unconsumed aeciospores, and bark fragments that dropped from rusted stems. Beginning of pupation was determined by a shortening and thickening of larvae, their immobility, and the appearance of black eye spots. The first adults emerged 14 to 36 (average 23) days after the first larvae began leaving aecia. If development proceeds similarly under natural conditions, roughly 30 to 40 days would be required for completion of the beetle's life cycle.

The beetles were not found on other plants in the vicinity of the pine stem rusts, although members of the family Phalacridae are known to frequent flowers of the Compositae in particular (Arnett 1973).

Beetle Infestations and Damage

At the Bucks Lake location where *P. harknessii* occurred on *Pinus ponderosa*, several hundred galls were observed annually on a stand of young trees covering approximately 0.5 ha. During the entire study period, not a

TABLE 2. Incubation period of *Phalacropsis dispar* in laboratory tests.

Year	National forest	Rust[1] fungus pine host	Collection date	Placed in beaker	Larvae moving from aecia	Pupation began	First adults	Total days from first larval maturity
1967	Toiyabe, California	Ps/Pj	7/14	7/17	7/20	7/24	8/3	14
1968	Toiyabe, California	Ps/Pj	6/22	6/25	7/1	7/5	7/17	16
1969	Dixie, Utah	Pf/Pp	6/23	6/25	7/3	7/22	7/28	25
1970	Plumas, California	Ph/Pp	5/26	5/28	6/3	6/18	6/29	26
1971	Plumas, California	Ph/Pp	5/30	6/6	6/12	6/16	7/14	36
1973	Plumas, California	Ph/Pp	5/28	5/28	6/4	6/11	6/26	22
1974	Plumas, California	Ph/Pp	5/23	5/25	5/31	6/4	6/18	18
1975	Toiyabe, Nevada	Pha/Pp	7/12	7/13	7/18	7/25	8/6	19

Ps/Pj = *Peridermium stalactiforme*/*Pinus jeffreyi*
Pf/Pp = *Peridermium filamentosum*/*Pinus ponderosa*
Ph/Pp = *Peridermium harknessii*/*Pinus ponderosa*
Pha/Pp = *Peridermium harknessii* (albino)/*Pinus ponderosa*

single gall was found without some evidence of beetle larval activity. Larvae reduced aeciospores and the underlying sporogenous mycelium to a mass of fecal debris (Fig. 2B) within approximately two weeks. The initial sporulation of young galls is usually a week or so later than older galls; these also become infested. In a single laboratory test (1971), four galls, 4 to 8 cm in diameter, produced an average of 130 adult beetles per gall.

A beetle infestation of similar intensity occurred on *Peridermium stalactiforme* on *Pinus jeffreyi* at Lee Vining Creek. Aecia matured about mid-June and were completely destroyed within about two weeks. Along a three km stretch of Lee Vining Creek, not one of the 20 limb-rusted trees examined annually remained free of the beetle. Aecial confluency with this rust is markedly less than with western gall rust, but few aecia were uninfested. Those that were uninfested were the more scattered aecia among needles toward the distal end of limbs. In two laboratory tests (1968 and 1971), a total of 3.9 m of typical rusted limbs yielded 3.4 adult beetles/cm and a total of 4.6 m of rusted limbs yielded 1.2 beetles/cm.

Beetle infestation of the Powell *Peridermium filamentosum* studied at Red Canyon was somewhat different from the infestations of *P. harknessii* and *P. stalactiforme* described above. With this rust fungus, aecia are tongue shaped and single with little confluency (compare Figs. 2A and 2C). Seldom did more than one beetle larva occur within a single aecium. Larvae consumed the basal mycelium of an aecium first and then moved into the upper part. Frequently the upper part of aecia remained untouched. Pressure from the growing fecal mass often burst the aecium at its base. It appeared that a single aecial mass was sufficient to rear a single larva. Usually, fewer than 50 percent of the aecia became infected on rusted limbs of the 12 trees observed annually. The amount of damage seemed to vary more from year to year with this rust than with *P. harknessii* and *P. stalactiforme*. In California, few Inyo *P. filamentosum* aecia were infested some years, but virtually all aecia became infested in other years.

The other pine stem rusts were studied less. Infestation of *P. stalactiforme* on *Pinus contorta* in the Sierra Nevada of California was as severe as that noted on *P. jeffreyi* at Lee Vining Creek. Infestation of the Coronado *Peridermium filamentosum* was similar to that of the other forms of *P. filamentosum*, although limited to a shorter sporulation period. *Cronartium comandrae* was studied little, and so the extent of infestation was not known. Observation of the beetle on *C. occidentale* on *Pinus monophylla* Torr. and Frem. was limited to a large outbreak of the rust near Monitor Pass, Alpine County, in the Sierra Nevada of California. During the three seasons observed, aecial spore masses were virtually destroyed by the beetle in all trees examined.

DISCUSSION

The beetle *Phalacropsis dispar* is reported here to consume the aeciospores and the aecial mycelium of all species of native western pine stem rust fungi except *Cronartium conigenum* (Pat.) Peterson and *C. comptoniae*, neither of which was investigated. Aecial fructifications not only provide food but also protective chambers for the larvae. Within several weeks' time, aecia may be completely ravaged of their content; only the peridial shell and masses of fecal debris remain. Based on laboratory tests and field observations, the life cycle of the beetle is completed in 30 to 40 days. Apparently, the beetle overwinters as an adult and emerges in the spring to mate and lay eggs as aecia of the rust fungi begin forming. The rarity of *P. dispar* in insect collections is further evidence it is highly specific to these rust fungi. The insects are abundant on pine stem rust fungi, but these fungi are rather obscure to insect collectors. Also, if they live on other fungi or the flowers of vascular plants as do other Phalacaridae, they probably would turn up more frequently in collections.

The distribution of *P. dispar* appears to be primarily south of the 40th parallel. North of the parallel, the niche becomes increasingly occupied by *Epuraea* spp. Some adults or larvae of *P. dispar* could be found in almost all areas where native pine stem rust fungi in the aecial sporulation state were studied. The beetle appeared, however, to be absent in some areas such as coastal California and northern Utah. R. S. Peterson (pers. comm.) has found *Phalacropsis* to be common to abundant on both the albino and orange-spored *Peridermium harknessii* in the Black Hills of South Dakota and Wyoming and in parts of Colorado.

Reduction of the aeciospore inoculum by *Phalacropsis dispar* was not determined in quantitative terms, but based on my observations, it can be a high percentage of the potential amount. Not only is there a reduction of spores already formed at the time larvae begin feeding, but consumption of the underlying sporogenous mycelium reduces the final quantity of spores produced as well as the length of the sporulation period. Quantitative field data are needed to establish what impact *P. dispar* has in reducing aeciospore inoculum and in the natural control of pine stem rust fungi. Nevertheless, all factors in the host-pathogen-environment interaction are of some importance.

Information on the aeciospore dispersal period for native western pine stem rust fungi is limited. R. S. Peterson (1959), studying spore release from *Peridermium harknessii* at high elevation sites in Colorado, found intermittent, but abundant, sporulation for one to two months. In a two-year study, G. W. Peterson (1973) trapped 88 and 91 percent of the season's total release of *P. harknessii* aeciospores during a two- and three-week period each May. The remainder (9 to 12 percent) was trapped through June. In Krebills's (1968) study of *C. comandrae* in the Rocky Mountain States, aeciospore dispersal began in late May, peaked in the last half of June, and usually continued in small amounts through summer. With increasing elevation, dispersal was delayed and the period shortened.

The tremendous mass of spores produced by the aecial state of the pine stem rust fungi is an evolutionary adaptation that increases the chance for survival of these propagules through the environmental hazards of dissemination. Aeciospores (annual inoculum) serve as the initial step in what is a long series of events leading to infection of pine. They also function in the spread of rust fungi over long distances, and a reduction in the inoculum load would seem to be important. In autoecious rust fungi, such as *Endocronartium harknessii* (*Peridermium harknessii*), reduction of the aecial inoculum is likely to be of more significance than it would be in heteroecious rust fungi, such as *C. coleosporioides* or *C. comandrae*, which have the uredinial multiplication phase. The Inyo and Powell forms of *P. filamentosum*, with aecia adapted to survive potentially long dry periods, could be severely affected by early destruction of aecia. Even with heteroecious rust fungi, in the more arid regions of the western United States where favorable moisture requirements for infection are likely to occur less frequently during the uredinial phase, intensity of infection by aeciospores would seem to be important. *Phalacropsis dispar* is possibly specific to native conifer stem rust fungi, including *C. occidentale*, which is similar in host range to *C. ribicola*. If *P. dispar* does not feed on the introduced *C. ribicola*, it may reveal a deficit in the natural control of this rust fungus in North America. From reports in the literature, there appears to be a larger diversity of secondary organisms that inhabit native western pine stem rusts (Wollenweber 1934, Powell 1971a,b,c,d,e, Byler et al. 1972b, Powell et al. 1972, Powell 1974, Hiratsuka et al. 1979, Tsuneda and Hiratsuka 1979, 1980) than inhabit *C. ribicola* blister rust (Mielke 1933, 1935, Kimmey 1969, Williams 1972, Furniss et al. 1972, Hungerford 1977, Hunt 1978). Members of the genus *Epuraea* evidently are widely distributed in the northwestern United States and western Canada (Hatch 1961, Parsons 1967, Powell 1971d, Powell et al. 1972). The aggressive *Epuraea obliquus* and *E. ovata*, obligate consumers of aeciospores of four different species of native pine stem rust fungi (Hubert 1923, Powell et al. 1972), were not reported by Furniss et al. (1972) to occur on *C. ribicola* blister rust cankers in northern Idaho. Both *E. obliquus* and *E. ovata* are known to exist in the eastern Oregon, northern Idaho, and western Montana areas (Hubert 1923, Hatch 1961). The absence of natural control of *C. ribicola* in western North America has been attributed primarily to a lack of host resistance (Bingham et al. 1971, Hoff and McDonald 1972). Byler et al. (1972a) provide evidence that secondary fungi and insects were primarily responsible for stabilizing populations of *Peridermium harknessii* at a low equilibrium position on coastal California pines. *Pinus radiata* and other coastal pine species become heavily infected with this rust fungus. Although these species are apparently highly susceptible to infection, resistance mechanisms probably provide tolerance (True 1938). Genetic drift of susceptibility from areas protected by an environment unfavorable for infection could account for part of this high susceptibility. The extent of natural control resulting from the activity of secondary organisms is a possible explanation for the reduced need for host resistance.

The rust fungi are well-known obligate parasites and have evolved with their hosts to a state of mutual survival. Considering the factors involved in rust disease epidemiology, it appears that secondary organisms would tend to reduce disease incidence and thus reduce selection for host resistance. The importance of secondary organisms should perhaps be placed more in the perspective of what disease incidence might be in their absence rather than as candidates for biological control above and beyond what occurs in a natural environment.

Literature Cited

Anderson, N. A., and D. W. French. 1964. Debarking jack pine infected with sweetfern rust. Plant Dis. Rept. 48:530–531.

Arnett, R. H., Jr. 1973. The beetles of the United States (A manual for identification). Amer. Entomol. Inst., Ann Arbor, Michigan. 1112 pp.

Bingham, R. T., R. J. Hoff, and G. I. McDonald. 1971. Disease resistance in forest trees. Ann. Rev. Phytopathol. 9:433–452.

Byler, J. W., F. W. Cobb, Jr., J. R. Parmeter, Jr. 1972a. Effects of secondary fungi on the epidemiology of western gall rust. Canadian J. Bot. 50:1061–1066.

———. 1972b. Occurrence and significance of fungi inhabiting galls caused by *Peridermium harknessii.* Canadian J. Bot. 50:1275–1282.

Carlson, C. E. 1978. Noneffectiveness of *Ribes* eradication as a control of white pine blister rust in Yellowstone National Park. USDA For. Serv. N. R. Rept. 78-18.

Casey, T. L. 1889–1890. Coleopterological notices. Ann. New York Acad. Sci. 5:89–144.

Coulson, R. N., and R. T. Franklin. 1970. The occurrence of *Dioryctria amatella* and other insects in *Cronartium fusiforme* cankers. Canadian Entomol. 102:353–357.

Dixon, C. S. 1978. A *Peridermium* rust associated with dwarf mistletoe on lodgepole pine. Unpublished thesis. Colorado State Univ. 100 pp.

Furniss, M. M., R. D. Hungerford, and E. F. Wicker. 1972. Insects and mites associated with western white pine blister rust cankers in Idaho. Canadian Entomol. 104:1713–1715.

Hanover, J. W. 1966. Tree improvement for disease resistance in western United States and Canada. Pages 53–66 *in* Breeding pest resistant trees. Proc. NATO-IUFRO Sym., Penn. St. Univ. 1964. Pergamon Press, Oxford, England. 505 pp.

Hatch, M. H. 1961. The beetles of the Pacific Northwest. Part III: Pselaphidae and Diversicornia 1. Univ. of Washington Press, Seattle. 503 pp.

Hiratsuka, Y., and J. M. Powell. 1976. Pine stem rusts of Canada. Canada Dep. Environ., For. Serv., Forestry Tech. Rep. 4. 83 pp.

Hiratsuka, Y., A. Tsuneda, and L. Sigler. 1979. Occurrence of *Scytalidium uredinicola* on *Endocronartium harknessii* in Alberta, Canada. Plant. Dis. Rept. 63:512–513.

Hoff, J. R., and G. I. McDonald. 1972. Stem rusts of conifers and the balance of nature. Pages 525–536 *in* Biology of rust resistance in forest trees. Proc. NATO-IUFRO Adv. Study Inst., Moscow, Idaho, 1969. USDA For. Serv. Misc. Publ. 1221. 681 pp.

Hubert, E. E. 1923. The life history of *Cronartium coleosporioides.* Unpublished manuscript. Div. For. Dis. Res., Washington Off. For. Serv. 76 pp.

Hungerford, R. D. 1977. Natural inactivation of blister rust cankers on western white pine. For. Sci. 23:343–350.

Hunt, R. S. 1978. Slugs feeding on *Cronartium* in British Columbia. Canadian For. Serv. Res. Note 34:21.

Kimmey, J. W. 1969. Inactivation of lethal-type blister rust cankers on western white pine. J. For. 67:296–299.

Krebill, R. G. 1968. *Cronartium comandrae* in the Rocky Mountain States. USDA For. Serv., Intermt. For. and Range Expt. Sta., Res. Pap. INT-40, 28 pp.

Kuhlman, E. G. 1981a. Mycoparasite effects of *Scytalidium uredinicola* on aeciospore production and germination of *Cronartium quercuum* sp. *fusiforme.* Phytopathology 71:186–188.

———. 1981b. Parasite interaction with sporulation by *Cronartium quercuum* subsp. *fusiforme* on loblolly and slash pine. Phytopathology 71:348–350.

Kuhlman, E. G., J. W. Carmichael, and T. Miller. 1976. *Scytalidium uredinicola* a new mycoparasite of *Cronartium fusiforme* on *Pinus.* Mycologia 68:1188–1194.

Kuhlman, E. G., and T. Miller. 1976. Occurrence of *Tuberculina maxima* on fusiform rust galls in the southeastern United States. Plant Dis. Rept. 60:627–629.

Leaphart, C. D., and E. F. Wicker. 1968. The ineffectiveness of cycloheximide and phytoactin as chemical controls of the blister rust disease. Plant Dis. Rept. 52:6–10.

LeConte, T. L. 1879. The Coleoptera of the alpine Rocky Mountain Regions—Part II. Bull. U.S. Geol. Survey 5(3,XXV):499–513.

Merkel, E. P. 1958. *Dioryctria* cone moth attack as related to cone rust of slash pine in North Florida. J. For. 56:651.

Mielke, J. L. 1933. *Tuberculina maxima* in western North America. Phytopathology 23:299–305.

______. 1935. Rodents as a factor in reducing aecial sporulation of *Cronartium ribicola.* J. For. 33:994–1003.

Mielke, J. L., and R. S. Peterson. 1967. Albino *Peridermium harknessii* in ponderosa pine. Plant Dis. Rept. 51:306–509.

Myren, D. T. 1964. Insects and fungi associated with *Cronartium fusiforme*-infected tissue and comparisons of the strength of infected and healthy wood. Phytopathology 54:902.

Nighswander, J. E., and R. F. Patton. 1965. The epidemiology of the jack pine-oak gall rust (*Cronartium quercuum*) in Wisconsin. Canadian J. Bot. 43:1561–1581.

Parsons, C. T. 1967. North American Nitidulidae (Coleoptera) IV. *Epuraea* associated with fungi on pine and oak. Canadian Entomol. 99:734–737.

Peterson, G. W. 1973. Dispersal of aeciospores of *Peridermium harknessii* in central Nebraska. Phytopathology 63:170–172.

Peterson, R. S. 1959. Pine gall rust in the Rocky Mountains. Dissertation. Univ. of Michigan. Diss. Abstr. 20(5)1557, 111 pp.

______. 1966. Limb rust damage to pine. USDA For. Serv., Intermt. For. and Range Expt. Sta., Res. Pap. INT-31, 10 pp.

______. 1968. Limb rust of pine: the causal fungi. Phytopathology 58:309–315.

Peterson, R. S., and F. F. Jewell. 1968. Status of American stem rusts of pine. Ann. Rev. Phytopathology 6:23–40.

Powell, J. M. 1971a. Fungi and bacteria associated with *Cronartium comandrae* on lodgepole pine in Alberta. Phytoprotection 52:45–51.

______. 1971b. Occurrence of *Tuberculina maxima* on pine stem rusts in western Canada. Canadian Plant Dis. Surv. 51:83–85.

______. 1971c. Incidence and effect of *Tuberculina maxima* on cankers of the pine stem rust, *Cronartium comandrae.* Phytoprotection 52:104–111.

______. 1971d. The arthropod fauna collected from the comandra blister rust, *Cronartium comandrae* on lodgepole pine in Alberta. Canadian Entomol. 103:908–918.

______. 1971e. Additional records of *Mycodiplosis* larvae (Diptera: Cecidomylidae) feeding on rust fungi. Canadian Plant Dis. Surv. 51:86–87.

______. 1974. The role of natural biological agents in controlling a pine stem rust (*Cronartium comandrae*). Blue Jay 32:75–79.

Powell, J. M., H. R. Wong, and J. C. E. Melvin. 1972. Arthropods collected from stem rust cankers of hard pines in western Canada. Canada Dept. Environ., Canadian For. Serv., Northern For. Res. Centre, Edmonton, Alberta. Rep. NOR-X-42, 19 pp.

Snell, W. H. 1919. Observations on the relation of insects to the dissemination of *Cronartium ribicola.* Phytopathology 9:451–464.

Toko, H. V., D. A. Graham, C. E. Carlson, and D. E. Ketcham. 1967. Effect of past *Ribes* eradications on controlling white pine blister rust in northern Idaho. Phytopathology 57:1010.

True, R. P. 1938. Gall development on *Pinus sylvestris* attacked by the Woodgate *Peridermium*, and morphology of the parasite. Phytopathology 28:24–49.

Tsuneda, A., and Y. Hiratsuka. 1979. Mode of parasitism of mycoparasite, *Cladosporium gallicola*, on western gall rust, *Endocronartium harknessii.* Canadian J. Plant Pathol. 1:31–36.

______. 1980. Parasitization of pine stem rust fungi by *Monocillium nordinii.* Phytopathology 70:1101–1103.

Tsuneda, A., Y. Hiratsuka, and P. T. Maruyama. 1980. Hyperparasitism of *Scytalidium uredinicola* on western gall rust, *Endocronartium harknessii.* Canadian J. Bot. 58:1154–1159.

Williams, R. E. 1972. Fungi associated with blister rust cankers on western white pine. Dissertation. Washington State Univ. 125 pp. Xerox Univ. Microfilms, Ann Arbor, Mich., No. 72-31308. Diss. Abstr. 33/05-B, p. 2434.

Wollenweber, H. W. 1934. *Fusarium bactridioides* sp. *nov.* associated with *Cronartium.* Science 79(2060):572.

Van Arsdel, E. P. 1961. Growing white pine in the Lake States to avoid blister rust. USDA For. Serv. Lake States For. Exp. Sta., Pap. 92, 11 pp.

Wong, H. R. 1972. *Dioryctria banksiella* (Lepidoptera: Pyralidae) in the western gall rust, *Endocronartium harknessii* (Basidiomycetes: Uredinales). Canadian Entomol. 104:251–255.

SPECIES-HABITAT RELATIONSHIPS IN AN OREGON COLD DESERT LIZARD COMMUNITY

David F. Werschkul[1]

Abstract.— The abundance and diversity of lizards in nine habitat types from Oregon were studied from May through October 1980. Eight species were from eight habitat types. The most common species were *Sceloporous occidentalis*, *Uta stansburiana*, *Sceloporous graciosus*, and *Cnemidophorus tigris*. *Phrynosoma douglassi* was uncommon and *Eumeces skiltonianus* was not observed. Temporary streams in nonbasaltic areas were the most productive habitat in terms of lizard abundance but sagebrush areas were the most productive habitat in terms of species diversity. No lizards were recorded from grassland conversion areas. The conflict between a land management policy that emphasizes both vegetation conversion and conservation of present wildlife stocks is discussed.

The herpetofauna of Malheur County, located in the extreme southeastern corner of Oregon, has been largely neglected in spite of the biological interest in this transition zone between the Great Basin and the cold desert areas of northern Oregon, Washington, and Idaho (Storm and Pimentel 1949, Ferguson et al. 1958, St. John 1980). The purpose of this study was to survey the herpetofauna and relate abundance and diversity to habitat type. Herein I report my findings on the structure of the lizard community. The abundance and diversity of amphibians and snakes is reported elsewhere (Werschkul 1980).

Study Area

The climate of southeastern Oregon is characterized by variation with short, hot summers, mean July temperature of 25 C, and long, cold winters, mean temperature between November and March of 4.6 C (Loy et al. 1976). Rainfall is highest in May, 40 mm, and lowest in August, 6 mm. A complex geologic area, early Miocene extrusions of basalt and rhyolite form the foundations for present formations (Kittleman et al. 1967, Kittleman 1973). Bisected by erosion, these volcanic platforms have formed elongate ridges and basins with deposition of alluvial materials along river channels. Plant communities from this high desert ecosystem, the juniper-sagebrush woodland extension of the Great Basin pinyon-juniper woodland (Detling 1968), have been classified by Franklin and Dyrness (1973), and, although big sagebrush (*Artemisia tridentata*)/bluebunch wheatgrass (*Agropyron spiratum*) is recognized as the climatic climax (Eckert 1957, Tueller 1962), native grasses have largely disappeared because of livestock grazing (Tueller 1962). Regardless, the composition of the plant community responds to local conditions and black sagebrush (*Artemisia arbuscula*) is found on shallow soils, shadscale (*Atriplex confertifolia*) and hopsage (*Grayia spinosa*) are common on xeric sites, and greasewood (*Sacrobatus vermiculatus*) dominates on sandy and alkaline sites.

Methods

The areas censused were bordered to the east by the Oregon-Idaho state line (117°05′W), to the west by the Alvord Desert (118°30′W), to the south by the Oregon-Nevada state line (42°00′N), and to the north by the Malheur River (44°00′N) from May through October 1980 (Fig. 1). Each census site was classified into one of nine habitat types depending on the composition of the plant community and the geologic and soil conditions. These habitat types were sagebrush, alkaline flats, grasslands, rocky areas of basaltic or nonbasaltic origin, temporary streams in basaltic or nonbasaltic areas, permanent streams, and sand dunes.

Sagebrush.— A composite category for sagebrush areas including higher elevation sites of sagebrush in association with bitterbrush (*Purshia tridentata*), juniper (*Juniperus occidentalis*), and mountain mahogany (*Cercocarpus ledifolius*); xeric sites with saltbrush (*Atriplex* sp.); and rocky areas with black sagebrush, as well as the more common plateau and basin regions with nearly pure stands of big sagebrush.

---

[1] Kalmiopsis Field Station, Agness, Oregon 97406.

Alkaline flats.— The shrub community from these ancient lakebeds, or playas, include shadscale, hopsage, and greasewood, although on extremely alkaline areas the vegetation was absent except on small (ca 10 m²) hummocks.

Grasslands.— Native grasses have largely disappeared because of livestock grazing. Range restoration projects, under the administration of the Vale District of the Bureau of Land Management, include seeding of crested wheatgrass (*Agropyron cristatum*) (Heady and Bartolome 1977), and it is these areas I censused during this study.

Rocky areas of basaltic origin.— Those rocky areas that included exposed bluffs, talus slopes of basaltic rubble, and the more recent basaltic extrusions of the smooth pahoehoe type.

Rocky areas of nonbasaltic origin.— A composite category that included areas as diverse as arkose sandstone and hard pyroclastic flows. Shrub cover was always sparse, less than one shrub stem per 25 m².

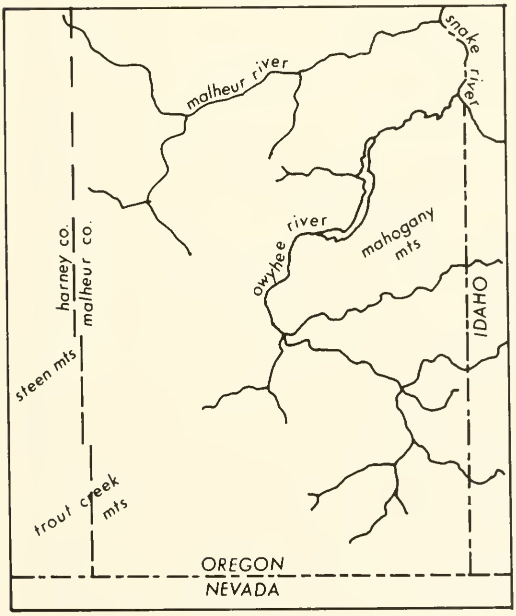


Fig. 1. Location of survey, Malheur County, Oregon.

Sand dunes.— Sandy areas devoid of vegetation except for border cover, usually greasewood or big sagebrush.

Temporary streams in basaltic areas.— Streams on ridges and steep slopes usually eroded to basalt; sandy areas might be present, but they were not extensive. The most common woody plants were willows (*Salix* spp.) and chokecherry (*Prunus* sp.).

Temporary streams in nonbasaltic areas.— Streams on relatively flat areas usually did not erode to basalt, although basaltic boulders were sometimes present. Woody plants were for the most part absent and the plant community was similar to that found in sandy, slightly alkaline areas and included greasewood, rabbitbrush (*Chrysothamnus* spp.), and Indian ricegrass (*Oryzopsis hymenoides*).

Permanent streams.— Those areas adjacent to permanent flowing water. Usually, a well-developed riparian community of willows, cottonwood (*Populus trichocarpa*), and hawthorn (*Crataegus* spp.) was present.

Lizards were censused by slowly walking (ca 0.5 m sec^{-1}) through areas noting those species present. Each census period lasted 20 minutes, and animal abundance was calculated as the number of animals seen per census period. In general, animals were not pursued or captured unless identification was uncertain. An area might be censused repeatedly, but no particular site was censused more than once. For example, Jordan Craters, a large expanse of recent basaltic extrusions (Kindschy and Maser 1978), was censused for 17 census periods, although no particular site was visited more than once. Most censuses were made during the morning, 0630–1030, and the afternoon, 1500–1900, although some censusing occurred at other times.

Malheur County, the study area, is large, approximately 2.6 million ha. Consequently, areas censused were representative of the habitats found there. Some areas were chosen because of reports of one species or another. To minimize error in determining species-habitat relationships, I censused each habitat type often enough, a total of 358 census periods or 4160 minutes, to reduce the impacts of season, time of day, and weather on animal activity (see Mayhew 1968, Parker and Pianka 1976). It is recognized that the *Phrynosoma* are probably underestimated and *Eumeces* may have been missed due to the survey technique used here.

Results and Discussion

Nine species comprise the lizard fauna of southeastern Oregon (Stebbins 1954, St. John 1980), eight of which were recorded during this study (Table 1). The most commonly observed species were *Sceloporous occidentalis, Uta stansburiana, Sceloporous graciosus*, and *Cnemidophorus tigris. Phyrnosoma douglassi* were uncommon, only two sightings, and *Eumeces skiltonianus* were not observed (but see St. John 1980). A total of 192 lizards or 0.5 animals per census period was recorded.

Habitat importance values were calculated in two ways: (1) as the percent of census sites per habitat type with at least one animal sighted, and (2) the average number of animals per successful census site (those sites with at least one animal sighting). As might be expected, these methods of estimating species-habitat values are positively correlated (Spearman Rank Correlation $= 0.48$; $p < 0.01$; $n = 29$), although some noteworthy exceptions exist. For example, for temporary streams in nonbasaltic areas *S. occidentalis* were found in 9.1 percent of the census sites, a relatively low value, but averaged 2.7 animals per successful census site. This may have resulted from the fact that, when large boulders (used for sunbathing) were present, *S. occidentalis* were more commonly observed than when large boulders were absent. Likewise, *S. graciosus* were relatively uncommon in sagebrush areas, 4.4 percent of the census sites, although relatively high numbers were found when encountered, 2.1 animals per successful census site. In this case, *S. graciosus* were uncommonly observed except where small mammal burrows were present. These lizards apparently use these burrows to aid in thermoregulation and to avoid predators. Conversely, although *Gambelia wislizeni* were commonly observed from temporary streams in nonbasaltic areas, 18.1 percent of census sites, numbers were always low, 1.5 animals per successful census site. *Gambelia wislizeni*, however, were not

Table 1. Occurrence of lizards from nine habitat types from Malheur County, Oregon.

			Habitat								
Species	n[a]	N[b]	Sagebrush	Alkaline flats	Grasslands	Rocky basalt	Rocky nonbasalt	Sand dunes	Temporary streams in basalt areas	Temporary streams in nonbasalt areas	Permanent streams
Crotaphytus bicinctores	10	20	1.3[c] 2.00[d]	—	—	7.1 1.00	—	—	—	15.1 2.60	—
Gambelia wislizeni	18	25	5.0 1.28	11.1 1.50	—	—	—	12.5 2.00	—	18.1 1.50	—
Sceloporus occidentalis	20	40	2.5 1.23	—	—	19.5 2.33	7.1 1.00	—	7.7 1.00	9.1 2.67	6.4 2.00
Sceloporus graciosus	16	32	4.4 2.10	33.3 2.30	—	6.8 1.00	—	—	—	—	—
Uta stansburiana	16	38	1.9 1.70	—	—	—	—	—	—	33.3 2.70	6.4 1.50
Phrynosoma douglassi	2	2	1.3 1.00	—	—	—	—	—	—	—	—
Phrynosoma platyrhinos	8	10	2.5 1.00	11.1 1.50	—	—	—	12.5 1.50	—	—	—
Cnemidophorus tigris	19	30	5.0 1.70	5.5 1.00	—	2.2 1.00	—	25.0 2.00	—	12.1 1.30	3.2 1.00

[a] Number of census periods with at least one animal sighting.
[b] Total number of animals sighted.
[c] Percent of census sites with at least one animal sighting.
[d] Average number of animals per successful census period.

observed in high numbers in any habitat (Table 1) and it is suspected that some spacing mechanism may be at work. Overall, when microhabitat characteristics cause clumping, such as the presence of boulders for S. *occidentalis* or small mammal burrows for S. *graciosus*, then the number of animals per successful census site tend to overestimate habitat importance.

Sagebrush habitat, in terms of species observed, was the most productive census area, with all eight species observed (Table 1). Grasslands, with no observations, was the least productive. Shrub cover is important in determining lizard distribution and abundance patterns by providing shaded areas needed for thermoregulation and as hiding sites from predators (Germano and Hungerford 1981). Shrub cover removal, by reducing the vertical and horizontal habitat stratification and shading and hiding areas, results in poor habitat for lizards. In terms of abundance, the habitat associated with temporary streams in nonbasaltic areas was the most productive and grasslands the least productive (Table 2). Each species had a preferred habitat (Table 1), and that associated with temporary streams in nonbasaltic areas was preferred by more species, three, than any other habitat type. Although sagebrush areas had the highest number of species observed, only *P. douglassi* preferred this habitat type (Table 1) and the average number of lizards seen per census period was comparatively low (Table 2).

The complete lack of observations of lizards in grasslands was unexpected. Although studies of lizard-habitat relationships in Arizona have shown low use of grasslands areas by most species, some species (e.g., Sonora spotted whiptail, *Cnemidophorus sonorae*) were more common in grasslands than elsewhere, and only a minority of species (4 of 9) went unrecorded in grasslands (Germano and Hungerford 1981). Two possible factors contributing to the lack of lizard sightings in the grasslands from this study were: (1) I ex cluded, as much as possible, any edge effects during censusing by picking grassland areas away from other habitat types and areas lacking sagebrush, boulders, or any other features causing habitat stratification, and (2), during the study year, rainfall was high, causing dense and tall stands of grasses to develop. This increased the technical difficulties associated with the walking transect survey and may have caused local lizard movements to habitats with open areas needed for foraging. It seems unlikely that all species of lizards avoided grasslands at all times, and some species may benefit from increases in the acreage of grasslands (Germano and Hungerford 1981). Census of areas with habitat discontinuities may have shown more use of grasslands by lizards than indicated here.

Still, to a large extent, lizards failed to use grasslands in this study area and a question arises relative to the economic necessity for expanding grasslands and the desire to conserve wildlife stocks. Grasslands, important for livestock production, were avoided by lizards in this study, and other plant communities, important to lizards, are unproductive for livestock. My findings suggest that, when

TABLE 2. The abundance and diversity of lizards for nine habitat types from Malheur County, Oregon. Diversity (H) is measured as the Shannon-Weaver index ($H = \Sigma -p_i \ln p_i$).

Habitat	Number of census periods	Number of species	H	Average number of lizards per census period
Temporary streams in nonbasaltic areas	33	5	1.41	1.97
Alkaline flats	18	4	0.97	1.17
Sand dunes	16	3	1.01	0.94
Rocky basaltic areas	46	4	0.83	0.61
Sagebrush	156	8	1.87	0.36
Permanent streams	31	3	0.94	0.26
Temporary streams in basaltic areas	13	1	—	0.08
Rocky nonbasaltic areas	14	1	—	0.07
Grasslands	18	0	—	0.00

multiple use management is desired, conversion areas need to maintain some characteristics of the native vegetation. For example, areas adjacent to temporary streams, frequently not suitable for crested wheatgrass, if conserved, would reduce the costs to the lizard community resulting from vegetation control programs. Importantly, dispersal corridors for the lizards, as well as valuable habitat for other wildlife, would be conserved. Finally, sagebrush areas are especially important to lizards, because all species were found to use this habitat. Management programs should follow the advice of Germano and Hungerford (1981) and clear variously shaped areas rather than attempt total removal of all nongrass vegetation.

ACKNOWLEDGMENTS

Bob Kindschy provided information on lizard locations in southeastern Oregon. This study was supported by the Bureau of Land Management (OR 910-CTO-14).

LITERATURE CITED

DETLING, L. E. 1968. Historical background of the flora of the Pacific Northwest. Univ. of Oregon Museum of Natural History. Eugene. 57 pp.

ECKERT, R. E., JR. 1957. Vegetation-soil relationships in some *Artemisia* types in northern Harney and Lake counties, Oregon. Unpublished dissertation. Oregon State College, Corvallis.

FERGUSON, D. E., K. E. PAYNE, AND R. M. STORM. 1958. Notes on the herpetofauna of Baker County, Oregon. Great Basin Nat. 18:63–65.

FRANKLIN, J. F., AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. Pacific NW Forest and Range Expt. Sta. Portland, Oregon. 417 pp.

GERMANO, D. J., AND C. R. HUNGERFORD. 1981. Reptile population changes with manipulations of Sonoran Desert shrub. Great Basin Nat. 41:129–138.

HEADY, H. F., AND J. BARTOLOME. 1977. The Vale rehabilitation program: the desert repaired in southeastern Oregon. USDA For. Serv. Resour. Bull. PNW-70, U.S. Pacific NW Forest and Range Expt. Sta. Portland, Oregon. 139 pp.

KINDSCHY, R. R., AND C. MASER. 1978. Jordan Craters research natural area. Federal Research Areas in Oregon and Washington: a guidebook for scientists and educators. Suppl. No. 7.

KITTLEMAN, L. R. 1973. Guide to the geology of the Owyhee region of Oregon. Museum of Natural History, Eugene, Oregon. Bull. No. 21. 61 pp.

KITTLEMAN, L. R., A. R. GREEN, G. H. HAGOOD, A. M. JOHNSON, J. M. MCMURRAY, R. G. RUSSELL, AND D. A. WEEDEN. 1967. Geologic map of the Owyhee region, Malheur County, Oregon. Museum of Natural History, Eugene, Oregon. Bull. No. 8.

LOY, W. G., S. ALLAN, C. P. PATTON, AND R. D. PLANK. 1976. An atlas of Oregon. Univ. of Oregon Press, Eugene, Oregon. 215 pp.

MAYHEW, W. W. 1968. Biology of desert amphibians and reptiles. Pages 195–356 *in* S. W. Brown, Jr., ed., Desert biology. Academic Press, New York.

PARKER, W. S., AND E. R. PIANKA. 1976. Ecological observations on the leopard lizard, *Crotaphytus wislizeni*, in different parts of its range. Herpetologica 32:95–104.

STEBBINS, R. C. Amphibians and reptiles of western North America. McGraw-Hill, New York. 528 pp.

ST. JOHN, A. D. 1980. Knowing Oregon reptiles. Salem Audubon Society, 36 pp.

TUELLER, P. T. 1962. Plant succession on two *Artemisia* habitat types in southeastern Oregon. Unpublished dissertation. Oregon State Univ., Corvallis.

STORM, R. M., AND R. A. PIMENTEL. 1949. Herpetological notes from Malheur County, Oregon. Great Basin Nat. 9:59–63.

WERSCHKUL, D. F. 1980. The amphibians and reptiles of southeastern Oregon. Unpublished report to the Vale District of the Bureau of Land Management. 56 pp.

PRELIMINARY INDEX OF AUTHORS OF UTAH PLANT NAMES

L. Matthew Chatterley,[1] Blaine T. Welsh,[1] and Stanley L. Welsh[1]

Abstract.— Presented herein is an index to approximately 800 authors of vascular plant names of Utah. A standardized abbreviation is presented for each author. These are listed alphabetically. Following each abbreviation is the full name and birth and death dates (where available) of each individual. In some cases the date of publication is given when biographical information is not known.

In compiling a preliminary list of Utah vascular plants (Welsh et al. 1981) an attempt was made to standardize abbreviations of author names, but the many inconsistencies throughout taxonomic literature suggested that additional work was needed. A list of all authors of Utah plant names, common abbreviations, and birth and death dates was begun. As the material accumulated, the potential usefulness of the information to others working in the field became apparent. There has been no previous single treatment listing the authors of Utah plant names and providing for some consistency of abbreviations. It is hoped that this guide will be a useful tool to all those who are concerned with the names of Utah plants. The name of the author of a particular taxon is considered to be a part of the plant name, and is especially useful in citation. The use of the author's name allows one to determine place of publication and other information necessary in taxonomic work.

Abbreviations are given first and then the full name. Birth and death dates (where available) are included to aid in correct identification of individuals. In some cases it has been impossible to find biographical information. We have included only the date of publication for those few individuals. We have chosen to list authors as they are cited in literature. Therefore, two or more authors may be listed together, and one author may appear in several places. This should facilitate easy access to bibliographic citations.

We have chosen to apply a double standard of abbreviation in some instances. Abbreviations of authors' names appearing separately are allowed longer designations than those where authors names are in combination with others (i.e., "T. & G." for Torrey and Gray, but "Torr." and "Gray" for the names when they stand alone).

Originally, abbreviations were to be based on the most common forms found in literature. Some authors names are sufficiently common in taxonomic literature that their abbreviations have become standard (i.e., Rydb., Wats., and A. Nels.). The names of other authors, often less well known or used only infrequently, were too varied, and it became apparent that a general rule was needed, even if it was an arbitrary one. It was not our purpose to rearrange a century of tradition, but strict adherence to a rigid standard was not considered practical.

During the process of this compilation the Royal Botanic Gardens, Kew, published the *Draft Index of Author Abbreviations: Flowering Plants* (Halliday et al. 1980). From that list some additional names and dates were obtained, but, most importantly, certain criteria for consistent abbreviations were adopted. It is not to be expected that the two lists will correspond exactly. We are only concerned with authors of Utah plant names and, with our center of focus on Utah plants, the scope is therefore much reduced.

The general principle followed has been not to abbreviate unless more than two letters could be saved by doing so (except where the tradition of taxonomic literature dealing with Utah flora has indicated a common and acceptable alternative; i.e., Marcus Eugene

---

[1] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Jones is "Jones," not "M.E. Jones"). Initials have been added to the abbreviation when more than one author having the same last name occurs on the list. This rule is generally followed, but when a father and son are both listed the son may be designated with an "f" (filius) following the last name. Accents, acutes, umlauts, and other diacritical marks have been omitted.

Some names included on the list are not those of taxonomists. Prior to Utah's existence as a state several government exploring expeditions made their way through portions of the region. Botanical information was obtained during these explorations and published in government records of the expeditions. Authors of those reports are cited in taxonomic literature and are included on this list also (John Charles Fremont, Howard Stansbury, William Emory, John Grubb Parke, Lorenzo Sitgreaves, Stephen Harriman Long, and others). The work of the late bibliographer of Utah botany, Earl M. Christensen (1967), was especially useful in obtaining information on obscure taxonomic publications and authors.

Checking of literature has been extensive. The volumes of *Taxonomic Literature* (Stafleu and Cowan 1976–81) were consulted, as was the three-volume set *Biographical Notes upon Botanists* (Barnhart 1965). Barnhart's work is a fairly complete reference of taxonomists publishing before the 1940s, and was especially helpful in providing biographical data on older authors. *Flora Europaea* (Tutin et al. 1964–80), an encyclopedic work on European plants, contains lists of authors and abbreviations at the end of each volume. Those lists were invaluable as sources of names and biographical data on many early European workers. Two lists of abbreviations published in state floras including information on many major botanical authors were also consulted (Keck 1970, Correll and Johnston 1970).

In many cases correct identification of an author was impossible without checking the original citation. Much time was spent consulting such standard taxonomic references as *Index Kewensis, Union List of Serials, Gray Herbarium Index,* and some bibliographic compilations such as Pritzel's *Thesaurus Literaturae Botanicae* and the four-volume work *Index to American Botanical Literature,* published by the Torrey Botanical Club.

Some information is still incomplete. Several older references have not been available to us, some recent author information remains sketchy, and, undoubtably, some names have been omitted entirely. Additionally, the discovering of new plant species and the renaming of others continues to be a vital business of contemporary taxonomists working with the Utah flora. This guide is, therefore, a preliminary documentation and we solicit help in obtaining corrections and additions. Address your comments to:

Herbarium Curator
Author Abbreviations
M. L. Bean Life Science Museum
Brigham Young University
Provo, Utah 84602

References

Barnhart, J. H. 1965. Biographical notes upon botanists. New York Botanical Gardens. 3 Vols. G. K. Hall & Co., Boston.

Christensen, E. M. 1967. Bibliography of Utah botany and wildland conservation. BYU Sci. Bull., Biol. Ser. 9(1):1–136.

Correll, D. S., and M. C. Johnston. 1970. Abbreviations of authors' names. Pages 1767–1794 *in* Manual of vascular plants of Texas. Contr. Texas Res. Foundation 6:i–1880.

Halliday, P., R. D. Meikle, J. Story, and H. Wilkinson. 1980. Draft index of author abbreviations. Royal Botanic Gardens, Kew.

Hunt, Rachel M. M. 1958 & 1961. Catalogue of botanical books. 2 Vols. Hunt Botanical Library, Pittsburgh.

Keck, D. D. 1970. Abbreviations of authors' names. Pages 1551–1576 *in* P. Munz and D. D. Keck, eds., A California flora. Univ. of California Press, Berkeley.

Pritzel, G. A. 1871–1877 (reprint 1972). Thesaurus literaturae botanicae. Otto Koeltz Antiquariat.

Stafleu, F. A., and R. S. Cowan. 1976. Taxonomic literature. 4 Vols. Utrecht, The Netherlands.

Torrey Botanical Club. 1969. Index to American botanical literature, 1886–1966. 4 Vols. G. K. Hall & Co., Boston.

Tutin, T. G., V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters, and D. A. Webb. 1964–80. Flora Europaea. 6 Vols. University Press, Cambridge.

Welsh, S. L., N. D. Atwood, S. Goodrich, E. Neese, K. H. Thorne, and B. Albee. 1981. Preliminary index of Utah vascular plant names. Great Basin Nat. 41:1–108.

INDEX OF AUTHORS

Abrams Leroy Abrams (1874–1956)
Achey Daisy Bird Achey (b. 1906)
Aellen Paul Aellen (1896–1973)
Agardh Carl Adolf Agardh (1785–1859)
Agardh f. Jacob Georg Agardh (1813–1901)
Ahles Harry E. Ahles (b. 1924)
Airy-Shaw Herbert Kenneth Airy-Shaw (b. 1902)
Ait. William Townsend Aiton (1766–1849)
All. Carl Allioni (1725–1804)
Al-Shebaz Ihsan A. Al-Shebaz
Ames Oakes Ames (1874–1950)
L. C. Anderson Loren C. Anderson (b. 1936)
Anderss. Nils Johan Andersson (1821–1880)
Andrz. Antoni Lukianowicz Andrzejowski (1784–1868)
Angstrom Johan Angstrom (1813–1879)
Arcangeli Giovanni Arcangeli (1840–1921)
Arnold (possibly a pseudonym; ca 1785)
Arv.-Touv. Jean Maurice Casimir Arvet-Touvet (1841–1913)
Asch. Paul Friedrich August Ascherson (1834–1913)
Asch. & Graebn. Paul Friedrich August Ascherson (1834–1913) and Karl Otto Robert Peter Paul Graebner (1871–1933)
Asch. & Mag. Paul Friedrich August Ascherson (1834–1913) and Paul Wilhelm Magnus (1844–1914)
Asch. & Sweinf. Paul Friedrich August Ascherson (1834–1913) and Sweinf.
Ashe William Willard Ashe (1872–1932)
Atwood Nephi Duane Atwood (b. 1938)
Austin Coe Finch Austin (1831–1880)
Babc. Ernest Brown Babcock (1877–1954)
Babc. & Stebbins Ernest Brown Babcock (1877–1954) and George Ledyard Stebbins, Jr. (b. 1906)
Babington Charles Cardale Babington (1808–1895)
Bailey Liberty Hyde Bailey (1858–1954)
D. K. Bailey David Kenneth Bailey (b. 1931)
V. L. Bailey Virginia Edith Bailey (b. 1908)
Baker John Gilbert Baker (1834–1920)
Baker Milo Samuel Baker (1868–1961)
Baker & Clausen Milo Samuel Baker (1868–1961) and Jens Christian Clausen (1891–1969)
Balbis Giovanni Battista Balbis (1765–1831)
Ball Carleton Roy Ball (1873–1958)
Banks Joseph Banks (1743–1820)
Banks & Sprengel Joseph Banks (1743–1820) and Kent Polycarp Joachim Sprengel (1766–1833)
Barbey William Barbey (1842–1914)
Barkley Fred Alexander Barkley (b. 1908)
T. M. Barkley Theodore Mitchell Barkley (b. 1934)
Barneby Rupert Charles Barneby (b. 1911)
Barneby & Holmgren Rupert Charles Barneby (b. 1911) and Noel Herman Holmgren (b. 1937)
Barratt Joseph Barratt (1796–1882)
Barton William Paul Gillon Barton (1786–1856)
Batch. Frederick William Batchelder (1838–1911)
Batsch August Johann Georg Karl Batsch (1761–1802)
Baumg. Johann Christian Gottlob Baumgarten (1765–1843)
Baxter Edgar Martin Baxter (b. 1903)
Beal William James Beal (1833–1924)
Beaman John H. Beaman (b. 1929)
Beauv. Baron Ambroise Marie Francois Joseph Palirot de Beauvois (1752–1820)
Bebb M. S. Bebb (1833–1895)
Becc. Odardo Beccari (1843–1920)
Beckwith Edward Griffin Beckwith (1818–1881)
Beetle Alan Ackerman Beetle (b. 1913)
Behr Hans Hermann Behr (1818–1904)
Bennett Arthur Bennett (1843–1929)
L. Benson Lyman David Benson (b. 1909)
Benson & Walkington Lyman David Benson (b. 1909) and D. L. Walkington (b. 1930)
Benth. George Bentham (1800–1884)
Benth. & Hook. George Bentham (1800–1884) and Joseph Dalton Hooker (1817–1911)
Bernh. Johann Jacob Bernhardi (1774–1850)
Besser Wilbert Swibert Joseph Gottlieb Besser (1784–1842)
Bessey Charles Edwin Bessey (1845–1915)
Betcke Ernest Friedrich (1815–1865)
Bicknell Eugene Pintard Bicknell (1859–1925)
Bieb. Friedrich August Marschall Bieberstein (1768–1826)
Bigelow Jacob Bigelow (1787–1879)
Blake Sidney Faye Blake (1892–1959)
Blank. Joseph William Blankinship (1862–1938)
Bluff & Fingerh. Mathias Joseph Bluff (1805–1837) and Karl Antoine Fingerhuth (1802–1876)
Blume Carl Ludwig von Blume (1796–1862)
Blytt Mathias Nurnsen Blytt (1789–1862)
Boeck. Johann Otto Boeckeler (1803–1899)
Boiss. Edmond Pierre Boissier (1810–1885)
Boissev. & Davids. Charles Hercules Boissevain (1893–1946) and Carol Davidson
Boissevain Charles Hercules Boissevain (1893–1946)
J. Boivin Joseph Robert Bernard Boivin (b. 1916)
Bolander Henry Nicholas Bolander (1831–1897)
Bong. August Heinrich Bongard (1786–1839)
F. Boott Francis Boott (1792–1863)
W. Boott William Boott (1805–1887)
Borbas Vincze von Borbas (1844–1905)
Boreau Alexander Boreau (1793–1875)
Borkh. Moritz Balthazar Borkhausen (1760–1806)
Borner C. J. B. Borner (b. 1880)
Bornm. Joseph Friedrich Nicolaus Bornmuller (1862–1948)
Botsch. Victor P. Botschantzev (b. 1910)
Bowden Wray Merrill Bowden (b. 1914)
Brack. William Dunlop Brackenridge (1810–1893)
Brand August Brand (1863–1930)
Brandegee Townsend Stith Brandegee (1843–1925)
M. Brandegee Mary Katharine Brandegee (1844–1920)
Branner & Coville John Casper Branner (1850–1922) and Frederick Vernon Coville (1867–1937)
A. Br. Alexander Carl Heinrich Braun (1805–1877)
Breitung August J. Breitung (b. 1913)
Brenckle & Cottam Jacob Frederick Brenckle (b. 1875) and Walter Page Cottam (b. 1894)
Brewer William Henry Brewer (1828–1910)
Brewer & Wats. William Henry Brewer (1828–1910) and Sereno Watson (1826–1892)
Briot Pierre Louis Briot (1804–1888)
Briq. John Isaac Briquet (1870–1931)
Britt. Nathaniel Lord Britton (1859–1934)
Britt. & Br. Nathaniel Lord Britton (1859–1934) and Addison Brown (1830–1913)
Britt. & Rose Nathaniel Lord Britton (1859–1934) and Joseph Nelson Rose (1862–1928)

Britt. & Rusby Nathaniel Lord Britton (1859–1934) and Henry Hurd Rusby (1855–1940)

Britt. & Shafer Nathaniel Lord Britton (1859–1934) and John Adolph Shafer (1863–1918)

B.S.P. Nathaniel Lord Britton (1859–1934), Emerson Ellick Sterns (1846–1926) and Justus Ferdinand Poggenburg (1840–1893)

R. Br. Robert Brown (1773–1858)

Buch.-Ham. Francis Buchanan-Hamilton (1762–1829)

Buch. Franz Georg Phillipp Buchenau (1831–1906)

Buchholz John Theodore Buchholz (1888–1951)

Buckley Samuel Botsford Buckley (1809–1884)

Bunge Alexander Andrejewitsch von Bunge (1803–1890)

Burgsd. Friedrich August Ludwig Burgsdorf (1747–1802)

Burman Johannes Burman (1706–1779)

Burman f. Nicolaas Laurens Burman (1734–1793)

Butters Frederic King Butters (1878–1945)

Butters & Abbe Frederic King Butters (1878–1945) and Ernst Cleveland Abbe (b. 1905)

Butters & St. John Frederic King Butters (1878–1945) and Harold St. John (b. 1892)

Canby William Marriot Canby (1831–1904)

Carr. Elie Abel Carriere (1818–1896)

Carruth James Harrison Carruth (1807–1896)

Cassidy James Cassidy (1844–1889)

Cav. Antonio Jose Cavanilles (1745–1804)

Chaix Dominique Chaix (1731–1800)

C. & S. Ludolf Karl Adalbert von Chamisso (1781–1838) and Diederich Franz Leonhard von Schlectendal (1794–1866)

Cham. Ludolf Karl Adalbert von Chamisso (1781–1838)

Chatel. Jean Jacques Chatelain (1736–1822)

Chaudhri Mohammad Nazeer Chaudri (b. 1932)

Chiov. Emilio Chiovenda (1871–1941)

Choisy Jacques Denys Choisy (1799–1859)

C. Chr. Carl Frederick Albert Christensen (1872–1942)

Chuang & Heckard Tsan-Lang Chuang (b. 1933) and Lawrence R. Heckard (b. 1923)

S. Clark Stephen L. Clark (b. 1940)

Clausen Jens Christian Clausen (1891–1969)

Clokey Ira Waddell Clokey (1878–1950)

Clover Elzada Urseba Clover (b. 1897)

Clover & Jotter Elzada Urseba Clover (b. 1897) and Mary Lois Jotter (b. 1914)

Cockerell Theodore Dru Alison Cockerell (1866–1948)

Conrad Solomon White Conrad (1779–1831)

Correll Donovan Stewart Correll (b. 1908)

Cory Victor Louis Cory (b. 1880)

Cosson Ernst Saint-Charles Cosson (1819–1889)

Cottam Walter Page Cottam (b. 1894)

Coult. John Merle Coulter (1851–1928)

Coult. & Nels. John Merle Coulter (1851–1928) and Aven Nelson (1859–1952)

Coult. & Rose John Merle Coulter (1851–1928) and Joseph Nelson Rose (1862–1928)

Covas Guillermo Covas (b. 1915)

Cov. Frederick Vernon Coville (1867–1937)

Craig Thomas Theodore Craig (b. 1907)

Crantz Heinrich Johann Nepomuk von Crantz (1722–1799)

Crepin Francois Crepin (1830–1903)

Cronq. Arthur John Cronquist (b. 1919)

Cronq. & Keck. Arthur John Cronquist (b. 1919) and David Daniels Keck (b. 1903)

Crosswhite Frank Samuel Crosswhite (b. 1940)

Curran Mary Katherine Curran (1844–1920)

Cyrillo Domenico Maria Leone Cyrillo (Cirillo) (1739–1799)

Daniels Francis Potter Daniels (1869–1947)

Danser Benedictus Hubertus Danser (1891–1943)

Darby John Darby (1804–1877)

Darlington Josephine Darlington (b. 1905)

Daston J. S. Daston (publ. 1946)

Daubs Edwin Horace Daubs (publ. 1965)

Daveau Jules Alexandre Daveau (1852–1929)

A. Davidson Anstruther Davidson (1860–1932)

R. J. Davis Ray Joseph Davis (b. 1895)

DC. Augustin Pyramus de Candolle (1778–1841)

A. & C. DC. Alphonse Louis Pierre Pyramus de Candolle (1806–1893) and Anne Casimir Pyramus de Candolle (1836–1918)

Decne. Joseph Decaisne (1807–1882)

Degl. Jean Vincent Yves Degland (1773–1841)

Dempster Lauramay Tinsley Dempster (b. 1905)

Dempst. & Ehrend. Lauramay Tinsley Dempster (b. 1905) and Friedrich Ehrendorfer (b. 1927)

Desf. Rene Louiche Desfontaines (1750–1833)

Desmarais Yves Desmarais (publ. 1952)

Desr. Louis Auguste Joseph Desrousseaux (1753–1838)

Desv. Auguste Nicaise Desvaux (1784–1856)

Detl. LeRoy Ellsworth Detling (1909–1967)

Dewey Chester Dewey (1784–1867)

Dieck Georg Dieck (1847–1925)

Diels Friedrich Ludwig Emil Diels (1874–1945)

A. Dietr. Albert Gottfried Dietrich (1795–1856)

D. Dietr. David Nathaniel Friedrich Dietrich (1800–1888)

Dippel Leopold Dippel (1827–1914)

D. Don David Don (1799–1841)

G. Don Georg Don (1798–1856)

Donn James Donn (1758–1813)

Dorn Robert D. Dorn (publ. 1977)

Dougl. David Douglas (1798–1834)

Drejer Solomon Thomas Nicolai Drejer (1813–1842)

E. Drew Elmer Reginald Drew (1865–1930)

Duchesne Antoine Nicolas Duchesne (1747–1827)

Dum-Cours. George Louis Marie Dumont de Courset (1746–1824)

Dumort. Barthelemy Charles Joseph Dumortier (1797–1878)

Dunal Michel Felix Dunal (1789–1856)

Dunn David Baxter Dunn (b. 1917)

Dunn & Harmon David Baxter Dunn (b. 1917) and William E. Harmon

Durand Elias Magloire Durand (1794–1873)

Dur. & Hilg. Elias Magloire Durand (1794–1873) and Theodore Charles Hilgard (1828–1875)

Durazzo Ippolito Durazzo (1750–1818)

Durieu Michel Charles Durieu de Maisonneuve (1796–1878)

Dziek. & Dunn Chester T. Dziekanowski and David Baxter Dunn (b. 1917)

Earle W. Hubert Earle (b. 1906)

Eastw. Alice Eastwood (1859–1953)

D. C. Eaton Daniel Cady Eaton (1834–1895)

Eckl. & Zeyh. Christian Frederick Ecklon (1795–1868) and Carl Ludwig Philipp Zeyher (1799–1858)

Edwards Sydenham Teast Edwards (1769–1819)

Edwin Gabriel Edwin (b. 1926)

Ehrend. Friedrich Ehrendorfer (b. 1927)
Ehrh. Friedrich Ehrhart (1742–1795)
Eichler Hansjoerg Eichler (b. 1916)
Ell. Stephen Elliott (1771–1830)
Ellison William L. Ellison (b. 1923)
Elmer Adolph Daniel Edward Elmer (1870–1942)
Emory William H. Emory (1811–1887)
Endl. Stephan Friedrich Ladislaus Endlicher (1804–1849)
Engelm. Georg Engelmann (1809⅛884)
Engelm. & Bigel. Georg Engelmann (1809–1884) and John Milton Bigelow (1804–1878)
Engler Heinrich Gustav Adolph Engler (1844–1930)
Engl. & Irm. Heinrich Gustav Adolph Engler (1844–1930) and Edgar Irmscher (1887–1968)
Engler & Prantl Heinrich Gustav Adolph Engler (1844–1930) and Karl Anton Eugene Prantl (1849–1893)
Erskine David S. Erskine (b. 1900)
Ewan Joseph Andorfer Ewan (b. 1909)
Farw. Oliver Atkins Farwell (1867–1944)
Fassett Norman Carter Fassett (1900–1954)
Fedde Friedrich Karl Georg Fedde (1873–1942)
Fern. Merritt Lyndon Fernald (1873–1950)
Ferris Roxana Judkins Ferris (b. 1895)
Fisch. Friedrich Ernst Ludwig von Fischer (1782–1854)
Fisch. & Mey. Friedrich Ernst Ludwig von Fischer (1782–1854) and Carl Anton Andrievic Meyer (1795–1855)
Fisch. & Trautv. Friedrich Ernst Ludwig von Fischer (1782–1854) and Ernst Rudolph Trautvetter (1809–1889)
Fisch., Mey., & Trautv. Friedrich Ernst Ludwig von Fischer (1782–1854), Carl Anton Andrievic Meyer (1795–1855) and Ernst Rudolph Trautvetter (1809–1889)
Flous M. Fernande Flous (b. 1908)
Flowers Seville Flowers (1900–1968)
Focke Wilhelm Olbers Focke (1834–1922)
Forb. & Hemsl. A. E. E. Forberg (b. 1851) and William Botting Hemsley (1843–1924)
Forbes James Forbes (1773–1861)
Forsskal Pehr (Peter) Forsskal (1732–1763)
Forster A. Forster (1810–1884)
Fosberg Francis Raymond Fosberg (b. 1908)
Fourn. Eugene Pierre Fournier (1834–1884)
Franchet Adrien Rene Franchet (1834–1900)
Franco Juao Manuel Antonio do Amaral Franco (b. 1921)
Franklin John Franklin (1786–1847)
Fraser John Fraser (1750–1811)
Frem. John Charles Fremont (1813–1890)
Fresen. Johann Baptist Georg Wolfgang Fresenius (1808–1866)
Fries Elias Magnus Fries (1794–1878)
Fritsch Karl F. Fritsch (1864–1934)
Gaertner Joseph Gaertner (1732–1791)
Gaertn., Mey. & Scherb. Joseph Gaertner (1732–1791), Bernhard Meyer (1767–1836) and Johannes Scherbius (1769–1813)
Galloway Leo A. Galloway (publ. 1975)
Gand. Michel Gandoger (1850–1926)
Garcke Christian August Friedrich Garcke (1819–1904)
Garrett Albert Osbun Garrett (1870–1948)
Gates Reginald Ruggles Gates (1882–1962)
C. Gay Claude Gay (1800–1873)
Gentry Howard Scott Gentry (b. 1903)
Geyer Carl Andreas Geyer (1809–1853)
Gilib. Jean Emmanuel Gilibert (1741–1814)
J. M. Gillett John Montagu Gillett (b. 1918)
Glad J. B. Glad (publ. 1971)
C. C. Gmel. Carl Christian Gmelin (1762–1837)
S. G. Gmel. Samuel Gottlieb Gmelin (1744–1774)
Godron Dominique Alexandre Godron (1807–1880)
Goldie John Goldie (1793–1886)
Goodding Leslie Newton Goodding (b. 1880)
Goodman George Jones Goodman (b. 1904)
Goodm. & Hitchc. George Jones Goodman (b. 1904) and Charles Leo Hitchcock (b. 1902)
Gopp. Heinrich Robert Goppert (1800–1884)
Gord. & Glend. George Gordon (1806–1879) and Robert Glendinning (fl. 1844–1858)
Gould Frank W. Gould (b. 1913)
Gould & Kapadia Frank W. Gould (b. 1913) and Zarir Kapadia (b. 1935)
Graebner Karl Otto Robert Peter Paul Graebner (1871–1933)
Graham Robert Graham (1786–1845)
Grant Alva Day Grant (b. 1920)
A. & V. Grant Alva Day Grant (b. 1920) and Verne Edwin Grant (b. 1917)
V. Grant Verne Edwin Grant (b. 1917)
Gray Asa Gray (1810–1888)
Gray, Wats. & Robins. Asa Gray (1810–1888), Sereno Watson (1826–1892) and Benjamin Lincoln Robinson (1864–1935)
S. F. Gray Samuel Frederick Gray (1766–1828)
Greene Edward Lee Greene (1843–1915)
Greenman Jesse Moore Greenman (1867–1951)
Greenm. & Roush Jesse Moore Greenman (1867–1951) and Eva Myrtelle Roush (b. 1886)
Griffith John William Griffith (1819–1901)
Griseb. August Heinrich Rudolf Grisebach (1814–1879)
Hackel Eduard Hackel (1850–1926)
Haenke Thaddaus Haenke (1761–1817)
Halacsy Eugene von Halacsy (1842–1913)
Hall Harvey Monroe Hall (1874–1932)
H. & C. Harvey Monroe Hall (1874–1932) and Frederic Edward Clements (1874–1945)
Hand.-Mazz. Heinrich von Handel-Mazzetti (1882–1940)
Hanks & Small Lenda Tracy Hanks (1879–1944) and John Kunkel Small (1869–1938)
C. A. Hanson Craig Alfred Hanson (b. 1935)
Harrington Harold David Harrington (b. 1903)
Hartman Carl Johan Hartman (1790–1849)
Harv. & Gray William Henry Harvey (1811–1866) and Asa Gray (1810–1888)
Hauman Lucien Hauman (1880–1965)
Hausskn. Heinrich Care Haussknecht (1838–1903)
Hawksworth & Wiens F. G. Hawksworth (fl. 1964) and Delbert Weins (b. 1935)
Haw. Adrian Hardy Haworth (1768–1833)
Hayden Ferdinand Vandeveer Hayden (1829–1887)
Heil Kenneth D. Heil (b. 1941)
Heimerl Anton Heimerl (1857–1942)
Heiser Charles Bixter Heiser (b. 1920)
Heller Amos Arthur Heller (1867–1944)
Hemsley William Botting Hemsley (1843–1924)

Henckel Leo Victor Felix Henckel von Donnersmarck (1785–1861)

Henderson Louis Forniquet Henderson (1853–1942)

Henrard Jan Theodoor Henrard (b. 1881)

L. Henry Louis H. Henry (1853–1903)

F. Hermann Frederick Joseph Hermann (b. 1906)

Herrmann Johann Herrmann (1738–1800)

Herter William Gustav Franz Herter (1884–1958)

Hess & Dunn Loyd W. Hess and David Baxter Dunn (b. 1917)

Hieron. Georg Hans Emmo Wolfgang Hieronymous (1846–1921)

Higgins Larry Charles Higgins (b. 1936)

Hildebr. Friedrich Hermann Gustav Hildebrand (1835–1915)

Hilend Martha Luella Hilend (b. 1902)

Hilend & Howell Martha Luella Hilend (b. 1902) and John Thomas Howell (b. 1903)

Hill John Hill (1716–1775)

A. S. Hitchc. Albert Spear Hitchcock (1865–1935)

Hitchc. & Chase Albert Spear Hitchcock (1865–1935) and Mary Agnes Chase (1869–1963)

C. L. Hitchc. Charles Leo Hitchcock (b. 1902)

Hitchc. & Maguire Charles Leo Hitchcock (b. 1902) and Bassett Maguire (b. 1904)

E. Hitchc. Edward Hitchcock (1793–1864)

Hoffm. George Franz Hoffman (1760–1826)

H. T. Holm Herman Theodor Holm (1854–1932)

A. & N. Holmgren Arthur Hermann Holmgren (b. 1912) and Noel Herman Holmgren (b. 1937)

Holmgren, Schultz & Lowrey Arthur Hermann Holmgren (b. 1912), Leila M. Schultz and Timothy K. Lowrey

N. Holmgren Noel Herman Holmgren (b. 1937)

N. & P. Holmgren Noel Herman Holmgren (b. 1937) and Patricia (nee Kern) Holmgren (b. 1940)

P. Holmgren Patricia (nee Kern) Holmgren

Holz. John Michael Holzinger (1853–1929)

Honck. Gerhard August Honckeny (1724–1805)

Hook. & Baker Joseph Dalton Hooker (1817–1911) and John Gilbert Baker (1834–1920)

Hook. William Jackson Hooker (1785–1865)

H. & A. William Jackson Hooker (1785–1865) and George Arnott Walker Arnott (1799–1868)

Hook. & Grev. William Jackson Hooker (1785–1865) and Robert Kaye Greville (1794–1866)

Hopkins Milton Hopkins (b. 1906)

Hoppe David Heinrich Hoppe (1760–1846)

Hornem. Jens Wilken Hornemann (1770–1841)

Host Nicolaus Thomas Host (1761–1834)

House Homer Doliver House (1878–1949)

J. T. Howell John Thomas Howell (b. 1903)

Howell Thomas Jefferson Howell (1842–1912)

Hu & Cheng Shiu-ying Hu (b. 1910) and Ching-yung Joyce Cheng (b. 1919)

Hubb. Frederic Tracy Hubbard (1875–1962)

Hudson William Hudson (1730–1793)

Hulten Oskar Eric Gunnar Hulten (1894–1981)

H. B. K. Friedrich Wilhelm Heinrich Alexander von Humboldt (1769–1859), Aime Jacques Alexandre Bonpland (1773–1858) and Karl Sigismund Kunth (1788–1850)

Huth Ernest Huth (1845–1897)

Hylander Nils Hylander (1904–1970)

Iltis Hugh Hellmut (b. 1925)

Isely Duane Isely (b. 1918)

Ives Joseph Christmas Ives (1828–1868)

Jacq. Nicolaus Jacquin (1727–1817)

James Edwin James (1797–1861)

Jarm. A. V. Jarmolenko (1905–1944)

Jepson Willis Linn Jepson (1867–1946)

Jepson & Bailey Willis Linn Jepson (1867–1946) and Liberty Hyde Bailey (1858–1954)

B. L. Johnson B. Lennart Johnson (b. 1909)

Johnston Ivan Murray Johnston (1898–1960)

J. R. Johnston John Robert Johnston (b. 1880)

Jones Marcus Eugene Jones (1852–1934)

Juz. Sergei Vasilievic Juzepczak (1893–1959)

Kar. & Kir. Grigorij Silic Karelin (1801–1872) and Ivan Petrovik Kirilow (1821 or 1822–1842)

Karsten Carl Wilhem Gustav Hermann Karsten (1817–1908)

Kaulf. Georg Friedrich Kaulfuss (1786–1830)

Kearney Thomas Henry Kearney (1874–1956)

Kearney & Peebles Thomas Henry Kearney (1874–1956) and Robert Hibbs Peebles (1900–1956)

Keck David Daniels Keck (b. 1903)

Kellogg Albert Kellogg (1813–1887)

Ker John Bellenden Ker (previously John Gawler) (1764–1842)

Kerner R. Anton Joseph Kerner von Marilaun (1831–1898)

Kiob. (publ. ca 1770)

Kit. Paul Kitaibel (1757–1817)

Kittell Marie Teresa Kittell (b. 1892)

W. Klein William Klein (publ. 1962)

Klotzsch Johann Friedrich Klotzsch (1805–1860)

Knerr Ellsworth Brownell Knerr (1861–1942)

K. Koch Karl Heinrich Emil Ludwig Koch (1809–1879)

Koch Wilhelm Daniel Joseph Koch (1771–1849)

Koehne Bernard Adalbert Emil Koehne (1848–1918)

Koeler George Ludwig Koeler (1765–1807)

Koenig Carl Dietrich Eberhard Koenig (1774–1851)

Koen. & Sims Carl Dietrich Eberhard Koenig (1774–1851) and John Sims (1740–1831)

Koidz. Genichi Koidzumi (1883–1953)

Komarov Vladimir Leontjevic Komarov (1869–1945)

Krap. Antonio Krapovickas (publ. 1970)

Krause Ernst Hans Ludwig Krause (1859–1942)

Kuhn Maximilian Friedrich Adelbert Kuhn (1842–1894)

Kukenthal Georg Kukenthal (1864–1955)

Kunth Karl Sigismund Kunth (1788–1850)

Kuntze Carl Ernst Otto Kuntze (1843–1907)

Kunze Gustav Kunze (1793–1851)

L'Her. Charles Louis de Brutelle L'Heritier (1746–1800)

Lag. Mariano Lagasca Y Segura (1776–1839)

Lag. & Rodr. Mariano Lagasca Y Segura (1776–1839) and Jose Demetris Rodriguez (1780–1846)

Lam. Jean Baptiste Antoine Pierre de Monnet de Lamark (1744–1829)

Lam. & DC. Jean Baptiste Antoine Pierre de Monnet de Lamark (1744–1829) and Augustin Pyramus de Candolle (1778–1841)

Lam. & Poir. Jean Baptiste Antoine Pierre de Monnet de Lamark (1744–1829) and Jean Louise Marie Poiret (1755–1834)

Lambert Alymer Bourke Lambert (1761–1842)

Lawson Charles Lawson (1794–1873)

Laxmann Erik G. Laxmann (1737–1796)

Ledeb. Carl Friedrich von Ledebour (1785–1851)

Lehm. Johann Georg Christian Lehmann (1792–1860)
Leiberg John Bernhard Leiberg (1853–1913)
Lej. Alexandre Louis Simon Lejeune (1779–1858)
Lellinger David Bruce Lellinger (b. 1937)
Lem. Charles Antoine Lemaire (1801–1871)
Lemmon John Gill Lemmon (1832–1908)
Lepage Ernest Lepage (b. 1905)
Less. Christian Friedrich Lessing (1809–1862)
H. Levl. Augustin Abel Hector Leveille (1863–1918)
Lewis & Szweykowski Frank Harlan Lewis (b. 1919) and Jerzy Szweykowski (b. 1925)
Leysser Friedrick Wilhelm Leysser (1731–1815)
Lilj. Samuel Liljeblad (1761–1815)
Lindl. John Lindley (1799–1865)
Lindl. & Gord. John Lindley (1799–1815) and George Gordon (1806–1879)
Lindl. & Paxt. John Lindley (1799–1865) and Joseph Paxton (1803–1865)
Lindsay George Edmund Lindsay (b. 1916)
Link Johann Heinrich Friedrich Link (1767–1851)
L. Carl von Linnaeus (1707–1778)
Little Elbert Luther Little Jr. (b. 1907)
Litv. Dmitrij Ivanovitsch Litvinov (1854–1929)
Lois. Jean Louis August Loiseleur-Deslongchamps (1774–1849)
Long Stephen Harriman Long (1784–1864)
Loudon John Claudius Loudon (1783–1843)
Lour. Joao de Loureiro (1717–1791)
Love Askell Love (b. 1916)
Love & Love Askell Love (b. 1916) and Doris Love (b. 1918)
Lund Peter Wilhelm Lund (1801–1880)
Macbr. & Payson James Francis Macbride (1892–1976) and Edwin Blake Payson (1893–1927)
Macbr. James Francis Macbride (1892–1976)
MacGregor Donald Macgregor (1877–1933)
Mack. Kenneth Kent Mackenzie (1877–1934)
Mack. & Bush Kenneth Kent Mackenzie (1877–1934) and Benjamin Franklin Bush (1858–1937)
Macmillan Conway Macmillan (1867–1929)
Macoun John Macoun (1831–1920)
Maguire Bassett Maguire (b. 1904)
Maguire & Cronq. Bassett Maguire (b. 1904) and Arthur John Cronquist (b. 1919)
Maguire & Holmgren Bassett Maguire (b. 1904) and Arthur Hermann Holmgren (b. 1912)
Maguire & Woodson Bassett Maguire (b. 1904) and Robert Everard Woodson (1904–1963)
Makino Tomitaro Makino (1862–1957)
Malte Malte Oscar Malte (1880–1933)
Manetti Guiseppe Manetti (1831–1858)
Mansfeld Rudolf Mansfeld (1901–1960)
Marcy Randolph Barnes Marcy (1812–1887)
Marshall Humphry Marshall (1722–1801)
W. T. Marshall William Taylor Marshall (1886–1957)
J. Martin James Stillman (b. 1914)
Martin Robert F. Martin (b. 1910)
Martius Carl Friedrich Phillipp von Martius (1794–1868)
Mason Herbert Louis Mason (b. 1896)
Mathias Mildred Esther Mathias (b. 1906)
Math. & Const. Mildred Esther Mathias (b. 1906) and Lincoln Constance (b. 1909)
Maxim. Carl Johann Maximowicz (1827–1891)
Maxon William Ralph Maxon (1877–1948)
McClatchie Alfred James McClatchie (b. 1906)
McClelland John McClelland (1805–1883)
McClintock & Epling Elizabeth May McClintock (b. 1912) and Carl Clawson Epling (1894–1968)
McKelvey Susan Delano McKelvey (b. 1883)
McVaugh Rogers McVaugh (b. 1909)
Medicus Friedrich Casimir Medicus (Medikus) (1736–1808)
Merr. Elmer Drew Merrill (1876–1956)
Mett. Georg Heinrich Mettenius (1823–1866)
Mey. & Scherb. Bernhard Meyer (1767–1836) and Johannes Scherbius (1769–1813)
C. A. Mey. Carl Anton Andreevic von Meyer (1795–1855)
E. Mey. Ernst Heinrich Friedrich Meyer (1791–1858)
F. G. Meyer Frederic Gustav Meyer (b. 1917)
Mez Carl Christian Mez (1866–1944)
Michx. Andre Michaux (1746–1802)
Miers John M. Miers (1789–1879)
Milde Carl August Julius Milde (1824–1871)
Miller Phillip Miller (1691–1771)
Milliken Jessie Milliken (b. 1887)
Millsp. Charles Frederick Millspaugh (1854–1923)
Mirbel Charles Francois Brisseau de Mirbel (1776–1854)
Moench Conrad Moench (1744–1805)
Moore Thomas Moore (1821–1887)
Moq. Christian Horace Benedict Alfred Moquin-Tandon (1804–1863)
Moretti Giuseppe L. Moretti (1782–1853)
Morong Thomas Morong (1827–1894)
Morot Louis Rene Marie Francois Morot (1854–1915)
Morton Conrad Vernon Morton (1905–1972)
Mosher Edna Mosher (Publ. 1915)
Muell.-Arg. Jean Mueller-Argoviensis (1828–1896)
Muenchh. Otto von Muenchhausen (1716–1774)
Muhl. Gotthiff Heinrich Ernest Muhlenberg (1753–1815)
Munro William Munro (1818–1889)
Munz Philip Alexander Munz (1892–1974)
Munz & Klein Philip Alexander Munz (1892–1974) and William McKinley Klein (b. 1933)
Murray John Andreas Murray (1740–1791)
Nakai Takenoshin Nakai (1882–1952)
Nash George Valentine Nash (1864–1921)
Necker Noel Martin Joseph de Necker (1729–1793)
Nees Christian Gottfried Daniel Nees von Essenbeck (1776–1858)
Nees & Mey. Christian Gottfried Daniel Nees von Essenbeck (1776–1858) and Franz Julius Ferdinand Meyen (1804–1840)
Neese & Welsh Elizabeth Janet Neese (b. 1934) and Stanley Larson Welsh (b. 1928)
A. Nels. Aven Nelson (1859–1952)
Nels. & Kennedy Aven Nelson (1859–1952) and Patrick Beveridge Kennedy (1874–1930)
Nels. & Macbr. Aven Nelson (1859–1952) and James Francis Macbride (1892–1976)
E. Nels. Elias Emanuel Nelson (1876–1949)
Nesom G. L. Nesom (publ. 1976)
Neuwied Maximilian Alexander Philipp Wied-Neuwied (1782–1867)
Nevski Sergei Arsenjevic Nevski (1908–1938)
Newberry John Strong Newberry (1822–1892)
Nicollet Jean Nicholas Nicollet (1786–1843)
Nieuwl. Julius Arthur Nieuwland (1878–1936)

Northstrom & Welsh Terry Edward Northstrom (b. 1945) and Stanley Larson Welsh (b. 1928)
J. B. S. Norton John Bitting Smith Norton (1872–1966)
Nutt. Thomas Nuttall (1786–1859)
O'Neill Hugh Thomas O'Neill (1894–1969)
Oakes William Oakes (1799–1848)
Oeder Georg Christian von Oeder (1728–1791)
Olney Stephen Thayer Olney (1812–1878)
Opiz Philipp Maximilian Opiz (1787–1858)
Ortega Casimiro Gomez Ortega (1740–1818)
Ortgies Karl Eduard Ortgies (1829–1916)
Osterh. George Everett Osterhout (1858–1937)
Ottley Alice Maria Ottley (b. 1882)
Ownbey Francis Marion Ownbey (b. 1910)
G. B. Ownbey Gerald Bruce Ownbey (b. 1916)
Pallas Peter Simon von Pallas (1741–1811)
Pamp. Renato Pampanini (1875–1949)
Parish Samuel Bonsall Parish (1838–1928)
Parke John Grubb Parke (publ. 1855)
Parker Kitty Lucille Parker (b. 1910)
Parl. Filippo Parlatore (1816–1877)
Parodi Lorenzo Raimundo Parodi (1895–1966)
Parry Charles Christopher Parry (1823–1890)
Pax Ferdinand Albin Pax (1858–1942)
Pax & K. Hoffm. Ferdinand Albin Pax (1858–1942) and Karl August Otto Hoffmann (1853–1909)
Paxton Joseph Paxton (1801–1865)
Payne Willard William Payne (b. 1934)
Payson Edwin Blake Payson (1893–1927)
Pease & Moore Arthur Stanley Pease (1881–1964) and Albert Hanford Moore (b. 1883)
Peck Morton Eaton Peck (1871–1959)
Peebles Robert Hibbs Peebles (1900–1956)
Pennell Francis Whittier Pennell (1886–1952)
Perry Matthew Calbraith Perry (1794–1858)
Pers. Christiaan Hendrick Persoon (1761–1836)
Petrak Franz Petrak (1886–1973)
Phil. Rudolf Amandus Philippi (1808–1904)
Pilger Robert Knud Friedrich Pilger (1876–1953)
Piller & Mitterp. Mathias Piller (1733–1788) and Ludwig Mitterpacher von Mitterburg (1734–1814)
Pilz G. E. Pilz (publ. 1978)
Piper Charles Vancouver Piper (1867–1926)
Piper & Beattie Charles Vancouver Piper (1867–1926) and Frederick Steere Beattie (1884–1939)
Planchon Jules Emile Planchon (1823–1888)
Poir. Jean Louis Marie Poiret (1755–1834)
Porsild Alf Erling Porsild (b. 1901)
C. L. Porter Charles Lyman Porter (b. 1889)
T. C. Porter Thomas Conrad Porter (1822–1901)
Port. & Coult. Thomas Conrad Porter (1822–1901) and John Merle Coulter (1859–1928)
Prain David Prain (1857–1944)
Prantl Karl Anton Eugene Prantl (1849–1893)
Presl Carel Borowag Presl (1794–1852)
J. & C. Presl Jan Swatopluk Presl (1791–1849) and Carel Borowag Presl (1794–1852)
Pringle James S. Pringle (b. 1937)
Pritz. George August Pritzel (1815–1874)
Purpus Joseph Anton Purpus (1860–1932)
Pursh Frederick Traugott Pursh (1774–1820)
Raf. Constantine Samuel Rafinesque-Schmaltz (1783–1840)
Ramaley Francis Ramaley (1870–1942)
Rattan Volney Rattan (1840–1915)
Raup Hugh Miller Raup (b. 1901)
Rauschert Stephen Rauschert (b. 1931)
Raven Peter Hamilton Raven (b. 1936)
Rech. Karl Rechinger (1867–1952)
Rech. f. Karl Heinz Rechinger (b. 1906)
Red. Pierre Joseph Redoute (1761–1840)
Rees Abraham Rees (1743–1825)
Regel Eduard August von Regel (1815–1892)
Rehder Alfred Rehder (1863–1949)
Rehmann Antoni Rehmann (1840–1917)
Reichenb. Heinrich Gottlieb Ludwig Reichenbach (1793–1879)
Retz. Anders Jahan Retzius (1742–1821)
Reveal James Lauritz Reveal (b. 1941)
Reveal & Brotherson James Lauritz Reveal (b. 1941) and Jack D. Brotherson (b. 1938)
Reveal, Broome, & Beatley James Lauritz Reveal (b. 1941), C. Rose Broome and Janice C. Beatley
Rich. Louis Claude Marie Richard (1754–1821)
A. Richards Alfred Richardson (publ. 1976)
Richards. John Richardson (1787–1865)
Richter Karl Richter (1855–1891)
Ricker Percy Leroy Ricker (1878–1973)
Riddell John Leonard Riddell (1807–1865)
J. W. Robbins James Watson Robbins (1801–1879)
Robins. Benjamin Lincoln Robinson (1864–1935)
Robins. & Fern. Benjamin Lincoln Robinson (1864–1935) and Merritt Lyndon Fernald (1873–1950)
Robins. & Greenm. Benjamin Lincoln Robinson (1864–1935) and Jesse More Greenman (1867–1951)
Roehl. Johann Christoph Roehling (1757–1813)
Roemer Johann Jacob Roemer (1763–1819)
R. & S. Johann Jacob Roemer (1763–1819) and Josef August Schultes (1773–1831)
Roezl Benito Roezl (1824–1885)
Rohrb. Paul Rohrbach (1847–1871)
Rollins Reed Clark Rollins (b. 1911)
Rollins & Shaw Reed Clark Rollins (b. 1911) and Elizabeth Anne Shaw (b. 1938)
Rose Joseph Nelson Rose (1862–1928)
Rose & Painter Joseph Nelson Rose (1862–1928) and Joseph Hannum Painter (1879–1908)
Rosend. Carl Otto Rosendal (1875–1956)
Rosend., Butters, & Lakela Carl Otto Rosendal (1875–1956), Frederic King Butters (1878–1945) and Olga Korhoven Lakela (b. 1890)
Roth Albrecht Wilhelm Roth (1757–1834)
Rothm. Werner Hugo Paul Rothmaler (1908–1962)
Rothr. Joseph Trimble Rothrock (1839–1922)
Rottb. Christen Friis Rottboell (1727–1797)
Rowley Gordon D. Rowley (b. 1921)
Rudd Velva E. Rudd (b. 1910)
Ruiz & Pavon Hipolito Ruiz (1754–1815) and Jose Antonio Pavon (1750–1844)
Rumpler Theodor Rumpler (1817–1891)
Rupr. Franz Josef Ruprecht (1814–1870)
Rydb. Per Axel Rydberg (1860–1931)
St. John Harold St. John (b. 1892)
St.-Yves Alfred Saint-Yves (1855–1933)
Salisb. Richard Anthony Salisbury (1761–1829)
Sarg. Charles Sprague Sargent (1841–1927)
Savi C. Gaetano Savi (1769–1844)
J. H. Schaffn. John Henry Schaffner (1866–1939)
Schauer Johann Conrad Schaure (1813–1848)

Scheele George Heinrich Adolf Scheele (1808–1864)
Schinz & R. Keller Hans Schinz (1858–1941) and Robert Keller (1854–1939)
Schkuhr Christian Schkuhr (1741–1811)
Schlecht. Diederich Franz Leonhard von Schlechtendal (1794–1866)
Schleicher Johann Christoph Schleicher (1768–1834)
Schleiden Matthias Jacob Schleiden (1804–1881)
Schneider Camillo Karl Schneider (1876–1951)
Schnitzl. Adalbert Carl Friedrich Schnitzlein (1814–1868)
Schoener Carol Susan Schoener (b. 1946)
Schott Heinrich Wilhelm Schott (1794–1865)
Schrader Heinrich Adolph Schrader (1767–1836)
Schrank Franz von Paula von Schrank (1747–1835)
Schreber Johann Christian Daniel von Schreber (1739–1810)
Schultes Josef August Schultes (1773–1831)
Schult. & Schult. Josef August Schultes (1773–1831) and Julius Hermann Schultes (1804–1840)
Schultz-Bip. Carl Heinrich Schultz-Bipontinus (1805–1867)
Schulz Otto Eugene Schulz (1874–1936)
K. Schum. Karl Moritz Schumann (1851–1904)
Schur Philipp Johann Ferdinand Schur (1799–1878)
Schweigger August Friedrich Schweigger (1783–1821)
Schweigg. & Koerte August Friedrich Schweigger (1783–1821) and Franz Koerte (1782–1845)
Schwein. Ludwig David von Schweinitz (1780–1834)
Scop. Giovanni Antonio Scopoli (1723–1788)
Scribn. Frank Lamson Scribner (1851–1938)
Scribn. & Merr. Frank Lamson Scribner (1851–1938) and Elmer Drew Merrill (1876–1956)
Scribn. & Sm. Frank Lamson Scribner (1851–1938) and Jared Gage Smith (1866–1925)
Scribn. & Will. Frank Lamson Scribner (1851–1938) and Thomas Albert Williams (1865–1900)
Seemann Berthold Carl Seeman (1825–1871)
Selander Nils Sten Edward Selander (1891–1957)
Sellow Friedrich Sellow (1789–1831)
Sendt. Otto Sendtner (1813–1859)
Sennen & Pau Frere Sennen (1861–1937) and Carlos Pau y Espanol (1857–1937)
Ser. Nicolas Charles Seringe (1776–1858)
Shear Cornelius Lott Shear (1865–1956)
Sheldon Edmund Perry Sheldon (b. 1869)
Shinn. Lloyd Herbert Shinners (1918–1971)
Shinz & Thell. H. Shinz (1858–1941) and Albert Thellung (1881–1928)
Sibth. John Sibthorp (1758–1796)
Sieb. & Zucc. Philipp Franz Siebold (1796–1866) and Joseph Gerhard Zuccarini (1797–1848)
Silliman Benjamin Silliman (1779–1864)
Silveus William Arento (b. 1875)
Sitgr. Lorenzo Sitgreaves (b. 1888)
Slosson Margaret Slosson (b. 1873)
Small John Kunkel Small (1869–1938)
Small & Cronq. John Kunkel Small (1869–1938) and Arthur John Cronquist (b. 1919)
Smiley Frank Jason Smiley (b. 1880)
C. P. Sm. Charles Piper Smith (1877–1955)
J. E. Sm. James Edward Smith (1759–1828)
J. G. Sm. Jared Gage Smith (1866–1925)
Smyth Bernard Bryan Smyth (1843–1913)
Sobol. Gregorius Fedorovitch Sobolevski (1741–1807)
Solbrig Otto Thomas Solbrig (b. 1930)
Soulange-Bodin Ettienne Soulange-Bodin (1774–1846)
Spach Edouard Spach (1801–1879)
Spegaz. Carlo Lingi Spegazzini (1858–1926)
Sprengel Kurt Polycarp Joachim Sprengel (1766–1833)
Stacey John William Stacey (1871–1943)
Standley Paul Carpenter Standley (1884–1963)
Stansb. Howard Stansbury
Stapf Otto Stapf (1857–1933)
Staudt Gunther Staudt (publ. 1961)
Sternb. Caspar Maria (Graf) von Sternberg (1761–1838)
Steudel Ernst Gottlieb von Steudel (1783–1856)
Stockwell William Palmer Stockwell (1898–1950)
Stokes Susan Gabriella Stokes (1868–1954)
Strother John Lance Strother (b. 1941)
Stuckey Ronald Lewis Stuckey (b. 1938)
Sturm Jakob W. Sturm (1771–1848)
Sudw. George Bishop Sudworth (1864–1927)
Suksd. Wilhelm Nikolaus Suksdorf (1850–1932)
Svenson Henry Knute Svenson (b. 1897)
Swallen Jason Richard Swallen (b. 1903)
Swartz Olof Peter Swartz (1760–1818)
Sweet Robert Sweet (1783–1835)
Syme John Thomas Irvine Boswell Syme (1822–1888)
Tateoka Tuguo Tateoka (b. 1931)
Taub. Paul Hermann Wilhelm Taubert (1862–1897)
Tausch Ignaz Friedrich Tausch (1793–1848)
Ten. Michele Tenore (1780–1861)
Thell. Albert Thellung (1881–1928)
Theobald William Louis Theobald (b. 1936)
Theobald & Tseng William Louis Theobald (b. 1936) and Chiao C. Tseng (publ. 1964)
Thieb. Arsenne Thiebaud de Berneaud (1777–1850)
H. J. Thompson Henry Joseph Thompson (b. 1921)
Thompson & Roberts Henry Joseph Thompson (b. 1921) and Roberts
Thompson Zadock Thompson (1796–1856)
Thuill. Jean Louis Thuillier (1757–1822)
Thunb. Carl Peter Thunberg (1743–1828)
Thurber George Thurber (1821–1890)
Tidestr. Ivar Frederick Tidestrom (1864–1956)
Tidestr. & Kittell Ivar Frederick Tidestrom (1864–1956) and Sister Marie Teresa Kittell (b. 1892)
Toft & Welsh Catherine Ann Toft (b. 1950) and Stanley Larson Welsh (b. 1928)
Tomb Andrew Spencer Tomb (b. 1943)
Torr. John Torrey (1796–1873)
Torr. & Frem. John Torrey (1796–1873) and John Charles Fremont (1813–1890)
T. & G. John Torrey (1796–1873) and Asa Gray (1810–1888)
Torr. & Hook. John Torrey (1796–1873) and William James Hooker (1785–1865)
Trautv. Ernst Rudolf von Trautvetter (1809–1889)
Trel. William Trelease (1857–1945)
Trev. Ludolf Christian Treviranus (1779–1864)
Trin. Carl Bernhard von Trinius (1778–1844)
Trin. & Rupr. Carl Bernhard von Trinius (1778–1844) and Franz Josef Ruprecht (1814–1870)
Turcz. Porphir Kiril Nicolas Stepanovich Turczaninow (1796–1864)
Turner Billie Lee Turner (b. 1925)
Underw. Lucien Marcus Underwood (1853–1907)
Vahl Martin Hendriksen Vahl (1749–1804)
Vail Anna Murray Vail (b. 1863)

Van Houtte Louis Van Houtte (1810–1876)
Vasey George Vasey (1822–1893)
Vasey & Scribn. George Vasey (1822–1893) and Frank Lamson Scribner (1851–1938)
Vell. Jose Mariano da Conceicao Velloso (1742–1811)
Vent. Etienne Pierre Ventenat (1757–1808)
Vill. Dominique Villars (1745–1814)
Vilm. Pierre Louis Francois Leveque de Vilmorin (1816–1860)
Vitman Fulgenzio Vitman (1728–1806)
Voss Andreas Voss (1857–1924)
Wagner Warren Herbert Wagner (b. 1920)
Wahl. Georg Wahlenberg (1780–1851)
Waldst. & Kit. Franz de Paula Adam von Waldstein (1759–1823) and Paul Kitaibel (1757–1817)
Wallr. Carl Friedrich Wilhelm Wallroth (1792–1857)
Walp. Gerhard Wilhelm Walpers (1816–1853)
Walter Thomas Walter (1740–1788)
Wangenh. Friedrich Adam Julius von Wangenheim (1747–1800)
Ward Lester Frank Ward (1841–1913)
Warder John Aston Warder (1812–1833)
Waterfall Umaldy Theodore Waterfall (1910–1971)
E. E. Watson Elba Emanuel Watson (1871–1936)
Wats. Sereno Watson (1826–1892)
Wats. & Coult. Sereno Watson (1826–1892) and John Merle Coulter (1851–1928)
T. J. Watson T. J. Watson (publ. 1977)
Webb Jonathan Edwards Webb ?? (publ. 1892)
D. A. Webb David Allardice Webb (b. 1912)
Weber Georg Heinrich Weber (1752–1828)
Weber & Mohr Georg Heinrich Weber (1752–1828) and Daniel Mathias Heinrich Mohr (1779–1808)
W. A. Weber William Alfred Weber (b. 1918)
Weigel Christian Ehrenfried von Weigel (1748–1831)
Weihe & Nees Carl Ernst August Weihe (1779–1834) and Christian Gottfried Daniel Nees von Essenbeck (1776–1858)
Weinm. Johann Anton Weinmann (1782–1858)
Welsh Stanley Larson Welsh (b. 1928)
Welsh & Atwood Stanley Larson Welsh (b. 1928) and Nephi Duane Atwood (b. 1938)
Welsh & Barneby Stanley Larson Welsh (b. 1928) and Rupert Charles Barneby (b. 1911)
Welsh & Goodrich Stanley Larson Welsh (b. 1928) and Sherel Goodrich (b. 1943)
Welsh & Johnston Stanley Larson Welsh (b. 1928) and Barry C. Johnston
Welsh & Moore Stanley Larson Welsh (b. 1928) and Glen Moore (b. 1917)
Welsh & Reveal Stanley Larson Welsh (b. 1928) and James Lauritz Reveal (b. 1941)
Welsh, Atwood, & Reveal Stanley Larson Welsh (b. 1928), Nephi Duane Atwood (b. 1938) and James Lauritz Reveal (b. 1941)
Wendl. Hermann A. Wendland (1823–1903)
Wheeler George Montague Wheeler (b. 1842)
Wherry Edgar Theodore Wherry (b. 1885)
Whipple Amiel Wicks Whipple (1818–1863)
White Theodore Greely White (1872–1901)
Wiegand & Backeberg Karl McKay Wiegand (1873–1942) and Curt Backeberg
Wiggers Friedrich Heinrich Wiggers (1746–1811)
Wiggins Ira Loren Wiggins (b. 1899)
Wight William Franklin Wight (1874–1954)
Wikstr. Johan Emanuel Wikstrom (1789–1856)
Wilkes Charles Wilkes (1798–1877)
Willd. Carl Ludwig von Willdenow (1765–1812)
L. O. Williams Louis Otho Williams (b. 1908)
Williams Thomas Albert Williams (1865–1900)
F. D. Wilson Frank D. Wilson (publ. 1963)
Winkler Hubert J. P. Winkler (1875–1941)
Wisliz. Friedrich Adolph Wislizenus (1810–1889)
With. William Withering (1741–1799)
Wittm. Marx Carl Ludewig Wittmack (1839–1929)
F. T. Wolf Franz Theodor Wolf (1841–1924)
S. J. Wolf & Packer S. J. Wolf and John G. Packer (b. 1929)
Wood Alphonso Wood (1810–1881)
Woodson Robert Everard Woodson (1904–1963)
Wooton Elmer Ottis Wooton (1865–1945)
Woot. & Standl. Elmer Ottis Wooton (1865–1945) and Paul Carpenter Standley (1884–1963)
Wormsk. Morton Wormskiold (1783–1845)
Wulfen Franz Xavier Wulfen (1728–1805)
Yates Harris Oliver Yates (b. 1934)
Yuncker Truman George Yuncker (1891–1964)
Zabel Hermann Zabel (1832–1912)

NEST SITE SELECTION IN RAPTOR COMMUNITIES OF THE EASTERN GREAT BASIN DESERT

Dwight G. Smith[1] and Joseph R. Murphy[2]

Abstract.— Measures of niche breadth and overlap were used to compare nest site selection in a community of 10 raptor species and the Raven nesting in the eastern Great Basin Desert. Three variables were examined: nest site type, elevation, and exposure. Results suggest a division of component raptor species into relatively abundant core species that show wide niche breadths and uncommon fringe species with narrow niche breadths. Differences in use of each resource are most pronounced along elevation gradient in which three guilds are evident that correspond to raptor species groupings that nest at higher, middle, and lower elevations. Each guild is comprised of a mix of core and fringe species. Raptor species with highest overlap along one or more nest site variables examined are separated by differences in activity patterns.

In this study we compare nest site selection in a community of 10 raptor species and the Raven (*Corvus corax*) nesting in the eastern Great Basin desert of Utah.

Nest site selection is a function of many variables, including proximity of foraging habitat, protection of nest and young, thermal environment of nest, and spatial interactions within the community. Nest sites of several raptor species in the eastern Great Basin have some common characteristics and appear similar, suggesting the occurrence of interspecific competition for available nest sites. Observations of occasional appropriation of Ferruginous Hawk (*Buteo regalis*) and Red-tailed Hawk (*Buteo jamaicensis*) nests by Great Horned Owls (*Bubo virginianus*); Raven nests by Great Horned Owls; and Great Horned Owl nests by Golden Eagles (*Aquila chrysaetos*) and Prairie Falcons (*Falco mexicanus*) indicate that nest site availability may be a limiting resource operating during periods of high raptor density (Smith and Murphy 1973). Conversely, partitioning of nest site resources may reduce competition among raptor species and facilitate coexistence.

We compared raptor nest site selection and extent of interspecific overlap using three nest site variables: type of placement, exposure, and elevation. The Raven is included in the comparison because it is a functional raptor, constructs nests that may be appropriated by raptor species, and competes for nesting sites with several raptor species.

Study Area

Long-term raptor studies began on a 7700 km² portion of the eastern Great Basin desert in winter 1966–1967. In previous papers we have presented observations on raptor population dynamics on a smaller 207-km² intensive study area (Smith and Murphy 1973) and described the response of large raptor species to fluctuations of their prey (Smith and Murphy 1979, 1981). Data for this study are from a 1170 km² segment of our original study area, which includes portions of Utah and Tooele counties in central Utah.

Topographically, the area is characterized by broad, flat, alkaline valleys separated by high, north-south oriented hills and ranges. Valley elevations range from 1460 to 1620 m and maximum elevations range from 1830 to 2440 m.

Climatically, the area is a northern cold desert (Shelford 1963). Annual precipitation averages 38 cm and monthly temperatures average from –5 C in January to 24 C in July, with wide daily and seasonal variations.

Two distinct vegetative associations are present. The desert shrub community occurs over the lower elevations and covers the valley floors. It consists of shrubs, herbs, and grasses, several of which form large, homo-

---

[1] Department of Biology, Southern Connecticut State College, New Haven, Connecticut 06515.

[2] Department of Zoology, Brigham Young University, Provo, Utah 84602.

Table 1. Yearly raptor populations nesting in the central Utah study area, 1967–1970.

Raptor species	1967	1968	1969	1970	Total nests
Golden Eagle	7	13	13	11	44
Ferruginous Hawk	15	28	34	13	90
Red-tailed Hawk	5	10	12	11	38
Swainson's Hawk	2	2	3	1	8
Prairie Falcon	1	1	1	2	5
Kestrel	3	3	2	2	10
Marsh Hawk	0	2	2	3	7
Great Horned Owl	6	14	16	10	46
Short-eared Owl	0	1	1	1	3
Burrowing Owl	1	2	4	3	10
Raven	4	5	5	3	17

geneous stands under certain edaphic soil conditions. Predominant desert shrub species include big sagebrush (*Artemisia tridentata*) on the better drained soils and greasewood (*Sarcobatus vermiculatus*) on the poorly drained valley floors. The well-drained slopes and hills support a dwarf conifer community of Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus monophylla*), which occur in stands of widely varying density.

A number of abandoned quarries, some of considerable size, are located in the foothills. Many have sheer cliffs ranging from 5–80 m in height. A few structures, all in various states of disrepair, were associated with some quarry sites. These and an abandoned gunnery tower at the U.S. Army Deseret Depot located in Rush Valley provided artificial nesting sites for some raptor species.

Methods

The study was conducted from November 1966 through July 1971. To locate nests, we subdivided the study area into 2.56-km² units, which were systematically searched in a rotating sequence at biweekly intervals throughout the nesting season. Foot searches of cliffs, rock outcrops, and juniper stands were supplemented by vehicle searches through desert shrub. Fixed-wing aircraft surveys were used two years to find nests but were of limited use due to minimum speed and altitude requirements. Fieldwork each year was from December through August. During this time a minimum of two days per week were spent on the study area, and total fieldwork per year averaged 1640 hours. Rotation of search areas throughout the nesting season ensured that all areas were checked several times, and we believe that we successfully located all raptor nests each year.

For each active nest located we recorded (1) elevation above sea level, (2) direction of exposure, and (3) type of placement. Nest site elevation was measured with a portable altimeter preset at USGS markers located on the study area. Recorded data were grouped in 50 m intervals. The nest site elevation variable permits comparison of how raptor species place their nests above the valley floors over which they hunted. Direction of nest site exposure was determined by orientation of a line projected at 90 degrees from a cliff wall or tree cavity through a nest center and grouped in one of eight equal subdivisions of the compass. Hillside tree and ground nests were classed by direction of slope. Nests on level ground were not included in exposure calculations except where nest site entrance orientation was obvious. We recognized 18 nest-site types including 5 cliff, 7 tree, 5 ground, and burrows (Table 2).

To compare raptor and Raven nest site selection, we used determinations of nest site niche breadth, overlap, and an average community overlap with respect to each of the three nest site variables.

Niche breadth of nest site selection was calculated using the standard information theoretic measure presented by Culver (1972):

$$\beta i = \frac{\sum_{j} N_{ij} \log N_{ij}}{\Sigma N_{ij} \, \Sigma N_{ij}} \log r$$

where N_{ij} is the abundance of species in category j and r is the number of categories. The value of β_i may range from 0 to 1.

To compare overlap of raptor and Raven nest site selection we used Horn's (1966) overlap index:

$$ih = \frac{[\sum_{j} (N_{ij} + N_{hj}) \log (N_{ij} + N_{hj}) - \sum_{j} N_{ij} \log _{ij} - {}_{j}N_{hj} \log N_{hj}]}{[(N_i + N_h) \log (N_i + N_h) - N_i \log N_i - N_h \log N_h]}$$

where N_{ij} is the value for species in category j, N_{hj} the value of species h in category j, N_i is the total of values for species in all categories and N_h is the total of values for species h in all categories. Overlap values may range from 0 to 1.

Average community overlap of each raptor species within the raptor community was calculated using the formula provided by Cody (1974):

$$\alpha\bar{x} \div \sum_{j}^{n-1} a_{ij}\, n-1$$

where $\bar{x}$ represents average community overlap of a species and all overlap values exclusive of a_{ii} are summed.

Dendrograms were constructed using both unweighted (UPGMA) and weighted (WPGMA) pair group cluster analyses (Sokal and Sneath 1963). Resultant dendrograms were similar and we have presented UPGMA in this paper.

RESULTS

Populations of raptors and ravens nesting on the study area from 1967 to 1970 are presented in Table 1. The Ferruginous Hawk was the most common raptor each year, varying from 13 nesting pairs in 1970 to 34 in 1969. Nesting populations of Great Horned Owls, Golden Eagles, and Red-tailed Hawks were approximately 50 percent smaller: Golden Eagles varied from 7 pairs in 1967 to 13 in 1968 and 1969, Great Horned Owls from 6 in 1967 to 16 in 1969, and Red-tailed Hawks from 5 pairs in 1967 to 12 in 1969. One other large raptor, the Swainson's Hawk (*Buteo swainsoni*) averaged two nesting pairs per year (range 1–3 pairs). Nesting populations of medium- and small-sized raptors were consistently low throughout the study period. Only one or two pairs of Prairie Falcons nested on the study area each year, and the only slightly more abundant Marsh Hawks (*Circus cyaneus*) nested in three of four study years (1968–70). Short-eared Owls (*Asio flammaeus*) were the least common raptor and only one nesting pair was found from 1968 to 1970. Raven nesting populations varied from 3 pairs in 1970 to 5 in 1968 and 1969. Although 6 of 11 species considered in this study were uncommon, they are characteristic components of nesting raptor populations in this portion of the eastern Great Basin.

TABLE 2. Percent distribution of raptor species in 18 nest site type categories.[a]

Nest Site Type	GE	GHO	FH	RtH	SwH	PF	MH	SpH	SeO	BuO	Ra
CLIFF SITES											
Quarry	26.3	19.5	–	7.9	–	30.0	–	40.0	–	–	11.5
20^+ m	22.7	6.5	–	7.9	–	10.0	–	–	–	–	23.6
5–19 m	47.5	43.4	–	36.8	–	60.0	–	30.0	–	–	5.9
5 m	–	2.2	3.2	5.3	–	–	–	–	–	–	59.0
Rock outcrop	4.5	–	24.6	–	–	–	–	–	–	–	–
TREE SITES											
Juniper (platform)	–	26.0	53.1	21.2	87.5	–	–	–	–	–	–
Juniper (cavity)	–	–	–	–	–	–	–	20.0	–	–	–
Pinyon Pine	–	2.2	2.1	7.9	–	–	–	–	–	–	–
Cliffrose	–	–	2.1	2.6	–	–	–	–	–	–	–
Cottonwood (platform)	–	–	1.0	5.3	12.5	–	–	–	–	–	–
Cottonwood (cavity)	–	–	–	–	–	–	–	10.0	–	–	–
Lombardy Poplar	–	–	–	5.3	–	–	–	–	–	–	–
GROUND SITES											
Sagebrush	–	–	7.5	–	–	–	74.4	–	33.3	–	–
Ricegrass	–	–	4.3	–	–	–	12.8	–	33.3	–	–
Horsebrush	–	–	2.1	–	–	–	–	–	–	–	–
Winter Wheat	–	–	–	–	–	–	12.8	–	33.3	–	–
Dry Wash	–	–	–	–	–	–	–	–	–	20.0	–
BURROW	–	–	–	–	–	–	–	–	–	80.0	–
Sample size (N)	44	46	90	38	8	5	7	10	3	10	17

[a] GE = Golden Eagle, GHO = Great Horned Owl, FH = Ferruginous Hawk, RtH = Red-tailed Hawk, SwH = Swainson's Hawk, PF = Prairie Falcon, MH = Marsh Hawk, SpH = Sparrow Hawk (American Kestrel), SeO = Short-eared Owl, BuO = Burrowing Owl, Ra = Raven.

Golden Eagles nested in 4 of 18 (23.5 percent) categories, all on cliff sites or rock outcrop (Table 2). Of the large raptors on the study area, Golden Eagles selected the narrowest range of nest sites. Comparatively, Ferruginous Hawks and Red-tailed Hawks selected the widest variety of nest sites, each using 9 of 18 (47.4 percent) types. Although both species used cliff and tree sites, major differences in type and frequency of use are evident. Over twice as many Red-tailed Hawk nests were located in cliffs (57.9 percent vs. 25.6 percent; d = 6.5; $P<0.05$). Over 55 percent of Red-tail nests were in cliffs greater than 5 m in height, whereas all Ferruginous Hawk nests were located in low cliffs (<5 m) and rock outcrops. Ferruginous Hawks chose tree sites more frequently (58.3 percent compared to 43.3 percent for Red-tailed Hawks), although both species most commonly constructed nests in junipers. Ferruginous Hawks but not Red-tailed Hawks also constructed nests on the ground (13.9 percent located in three of the four Great Basin Desert shrub communities available).

Great Horned Owls were found in 6 of 18 (13.5 percent) nest-site types, all of which were in cliffs and junipers. Golden Eagles, Prairie Falcons, and Ravens nested exclusively in cliff nest site types, and Swainson's Hawks were restricted to juniper and cottonwood sites. The two smallest raptors on the study area, the American Kestrel (*Falco sparverius*) and Burrowing Owl (*Athene cunicularia*) nested only in cavities, the former in cliffs (70 percent) and trees (30 percent) and the latter in burrows.

Two other species that used a narrow range of nest site types were the Marsh Hawk and Short-eared Owl. Both selected nest sites in desert shrub communities.

Raptor nest site locations in nine elevation categories are presented in Table 3. Although Golden Eagle nest sites were found in eight of nine elevation categories, ranging from 1460 to 1910 m, 78.5 percent were located at elevations greater than 1680 m. On the average, Golden Eagle nests were located at higher elevations than those of any other raptor in the study area. Great Horned Owls and Red-tailed Hawks were most similar to the Golden Eagle in nest site placement.

Great Horned Owl nests were found at all elevations, although most (82.5 percent) were located in elevations greater than 1600 m. Red-tailed Hawk nests were found in 8 of 9 (88.9 percent) elevation categories and also were primarily located at higher elevations. Comparatively, nests of two other large raptor species, the Swainson's Hawk and Ferruginous Hawk, were restricted to middle and lower elevations. A total of 85.1 percent of all Ferruginous Hawk nests were found between 1511 and 1660 m and none were placed at elevations higher than 1710 m; All Swainson's Hawk nests were found at elevations between 1460–1610 m. Nest sites of Ravens had the highest average elevation. All were above 1711 m and 94.1 percent were at elevations greater than 1761 m. Nest sites of Prairie Falcons were limited to middle elevations from 1611 to 1760 m, but three species, the Marsh Hawk, Short-eared Owl and Burrowing Owl nested exclusively in lower ele-

Table 3. Percent distribution of raptor species nests in nine elevation categories. Elevation in meters.

Species[a]	1460–1510	1511–1560	1561–1610	1611–1660	1661–1710	1711–1760	1761–1810	1811–1860	1861–1910	Number of nests
GE	4.5	0.0	2.3	4.5	22.7	29.5	15.9	6.8	13.6	44
GHO	4.3	4.3	8.7	13.0	21.7	26.1	10.9	4.3	6.5	46
FH	5.3	21.3	45.7	18.1	9.6	0.0	0.0	0.0	0.0	90
RtH	2.6	5.3	5.3	31.6	23.7	13.2	15.8	2.6	0.0	38
SwH	12.5	25.0	62.5	0.0	0.0	0.0	0.0	0.0	0.0	8
PF	0.0	0.0	0.0	20.0	40.0	40.0	0.0	0.0	0.0	5
MH	57.1	28.6	14.3	0.0	0.0	0.0	0.0	0.0	0.0	7
SpH	0.0	0.0	0.0	10.0	50.0	0.0	30.0	10.0	0.0	10
SeO	33.3	66.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
BuO	30.0	70.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10
Ra	0.0	0.0	0.0	0.0	0.0	5.9	29.4	47.1	17.6	17

[a] GE = Golden Eagle, GHO = Great Horned Owl, FH = Ferruginous Hawk, RtH = Red-tailed Hawk, SwH = Swainson's Hawk, PF = Prairie Falcon, MH = Marsh Hawk, SpH = Sparrow Hawk (American Kestrel), SeO = Short-eared Owl, BuO = Burrowing Owl, Ra = Raven.

vations, below 1610 m for the Marsh Hawk and below 1560 m for the latter two species.

A summary of distribution of raptor nests in eight exposure categories is presented in Table 4. Golden Eagles, Great Horned Owls, Ferruginous Hawks and Red-tailed Hawks had exposures in all eight categories, although each exhibited higher frequencies for certain exposures. Thus, 57.5 percent of all Golden Eagle nests had exposures from WNW-NNE but 52.5 percent of Great Horned Owl nests had WSW-WNW exposures. Exposure preferences of Ferruginous Hawks and Red-tailed Hawks were slightly less definitive, with the former showing highest ESE nest site exposure and the latter WSW. The two raptor species that nest exclusively in cliff and quarry cavities, the Raven and Prairie Falcon, both had maximum WNW nest site exposures. Short-eared Owls exhibited the narrowest range of nest site exposure, with all nests at ENE and ESE, but this may reflect the small sample size for this species.

Nest site niche breadth.— Niche breadth represents the range or diversity of a species along a resource gradient. Niche breadth values of raptor species along each variable are presented in Table 5.

A significant positive correlation between relative abundance of raptor species and niche breadth (β) was found for each of the nest site variables examined, i.e., type (T), elevation (E), and exposure (X), ($r = 0.62$, $t = 2.36$, $P < 0.05$ for β_T; $r = 0.63$, $t = 2.44$, $P < 0.05$ for β_E; and $r = 0.72$, $t = 3.12$, $P < 0.05$, for β_X), suggesting that the most common raptor species select the widest range of nesting sites. The Golden Eagle ranked eighth in range of nest site type (β_T) selection and tenth in nest site elevation (β_E) and had the widest breadth of nest site exposure selection (β_X). The three other most abundant raptors, the Great Horned Owl, Ferruginous Hawk, and Red-tailed Hawk, consistently ranked highest along each variable. If we assume that abundance of the large raptor species reflects their dominance, this is consistent with the predictions of Levins (1968) and McNaughton and Wolf (1970) that dominant community species occupy broader niches. The American Kestrel ranked sixth or seventh along each variable and showed broader values of nest site type and exposure but not elevation than the average β values of all species. Another middle-ranked species, the Raven, had a broad β_X but narrow β_T and β_E. It is widely distributed in this part of the Great Basin desert.

Five less common raptor species, the Prairie Falcon, Swainson's Hawk, Marsh Hawk, Short-eared Owl, and Burrowing Owl, showed β values well below the average in each variable. All showed narrow ranges in one or more of the nest site variables examined.

Niche overlap.— Niche overlap was calculated for all species pairs for each variable. Overlap values provide a measure of the potential impact one species may have on another. Patterns of overlap and community structure are best illustrated by dendrograms (Cody 1974), which show how species combinations that closely overlap along a

Table 4. Percent distribution of raptor nests in eight exposure categories.

Species[a]	WSW	WNW	NNW	NNE	ENE	ESE	SSE	SSW	Number of nests
GE	15.0	17.5	22.5	17.5	7.5	5.0	7.5	7.5	40
GHO	29.5	22.7	6.8	2.3	2.3	11.4	6.8	18.2	44
FH	21.6	2.7	8.1	2.7	6.8	27.0	16.2	14.9	74
RtH	23.7	10.5	2.6	7.9	5.3	18.4	18.4	13.2	38
SwH	12.5	0.0	0.0	25.0	25.0	37.5	0.0	0.0	8
PF	40.0	40.0	20.0	0.0	0.0	0.0	0.0	0.0	5
MH	0.0	42.9	0.0	28.6	28.6	0.0	0.0	0.0	7
SpH	10.0	10.0	40.0	0.0	10.0	20.0	10.0	0.0	10
SeO	0.0	0.0	0.0	0.0	66.6	33.3	0.0	0.0	3
BuO	0.0	0.0	14.3	0.0	0.0	57.1	14.3	14.3	7
Ra	23.5	41.2	11.8	0.0	11.8	5.9	0.0	5.9	17

[a] GE = Golden Eagle, GHO = Great Horned Owl, FH = Ferruginous Hawk, RtH = Red-tailed Hawk, SwH = Swainson's Hawk, PF = Prairie Falcon, MH = Marsh Hawk, SpH = Sparrow Hawk (American Kestrel), SeO = Short-eared Owl, BuO = Burrowing Owl, Ra = Raven.

resource dimension will form clusters or guilds. Community dendrograms for each nesting site dimension are presented in Figure 1. Each guild represents a group of species that exploit a specific nest site dimension in a similar manner.

Inspection of the nest site type (NST) dendrogram reveals four guilds, the largest (Guild A) containing six species and the smallest just one (Guild D). Subdivisions within the Guild A are, however, readily apparent: one shows close similarity of NST selection by the Golden Eagle and three other cliff-nesting raptors, Raven, and Prairie Falcon, and the second subdivision shows a close relationship between Great Horned Owls and Red-tailed Hawks. The frequent appropriation of Golden Eagle and Raven nests by Prairie Falcons and *Buteo* nests by Great Horned Owls contribute a significant percentage of the overlap and resulting structure of Guild A. Guild B pairs the Ferruginous and Swainson's hawks and illustrates isolating differences between these and the other large raptor species with respect to selection of nest type. The Marsh Hawk and Short-eared Owl both nest in desert shrub and occupy a separate NST guild. The Burrowing Owl is the only raptor species utilizing burrows for nest sites and is the sole member of its guild.

Both UPGMA and WPGMA dendrograms show the Ferruginous and Swainson's hawk combination closer to the Marsh Hawk and Short-eared Owl guild than Guild A containing the other large raptors. This is inconsistent with observational data: although 14 percent of Ferruginous Hawk nests were ground sites located in desert shrub, another 53 percent were in Juniper and the remainder on either rock outcrops or artificial structures. All Swainson's Hawk nests were located in trees. On the basis of overlap values, Ferruginous Hawks actually were closer to the Great Horned Owl–Red-tailed Hawk guild than the Marsh Hawk–Short-eared Owl guild (average pooled θ values of 0.6994 and 0.3823, respectively).

Clustering is maximal in the nest site elevation (NSF) dendrogram in which two guilds are evident. Golden Eagles are placed in Guild A, along with Great Horned Owls, Red-tailed Hawks, Prairie Falcons, American Kestrels, and Ravens. Raptor species composition of Guild A is identical to Guild A of NST dendrogram and species composition of Guild B corresponds to NST Guilds B, C, D. The two NSE guilds neatly separate raptor species that nest at middle and low elevations from those that select nest sites at comparatively higher elevations. NSE Guild B may be further subdivided into a cluster of two raptor species, the Ferruginous and Swainson's hawks, which nested at middle elevations in the knolls and foothills, and the cluster of three raptor species, the Marsh Hawk, Short-eared Owl, and Burrowing Owl, which nested in the valleys.

Two guilds are also formed in the nest site exposure (NSX) dendrogram. Raptor species composition of these guilds reveals interesting similarities and differences when compared to NST and NSE dendrograms previously examined. Differences in NSX preferences split the Ferruginous Hawk-

TABLE 5. Niche breadth parameters of nest site dimensions.[1]

Species	Number of nests[2]	Nest type β_T	Nest elevation β_E	Nest exposure β_X
Golden Eagle	44	.4581 (8)	.8241 (10)	.9439 (11)
Great Horned Owl	46	.4679 (9)	.9043 (11)	.8625 (8)
Ferruginous Hawk	90	.5033 (10)	.6268 (8)	.8870 (9)
Red-tailed Hawk	38	.6312 (11)	.8030 (9)	.9929 (10)
Swainson's Hawk	8	.1280 (1)	.4097 (3)	.6352 (5)
Prairie Falcon	5	.3050 (4)	.4801 (5)	.5073 (2)
Marsh Hawk	7	.2706 (3)	.4351 (4)	.5189 (3)
American Kestrel	10	.4347 (7)	.5317 (6)	.7740 (7)
Short-eared Owl	3	.3731 (6)	.2897 (2)	.3061 (1)
Burrowing Owl	10	.1699 (2)	.2780 (1)	.5551 (4)
Raven	17	.3637 (5)	.5403 (7)	.7422 (6)
Average (all species)		.3734	.5566	.7023

[1] Figures in parentheses indicate rank within parameter.

[2] Sample sizes used in nest site exposure determinations differ as follows: Golden Eagle, 40; Ferruginous Hawk, 74.

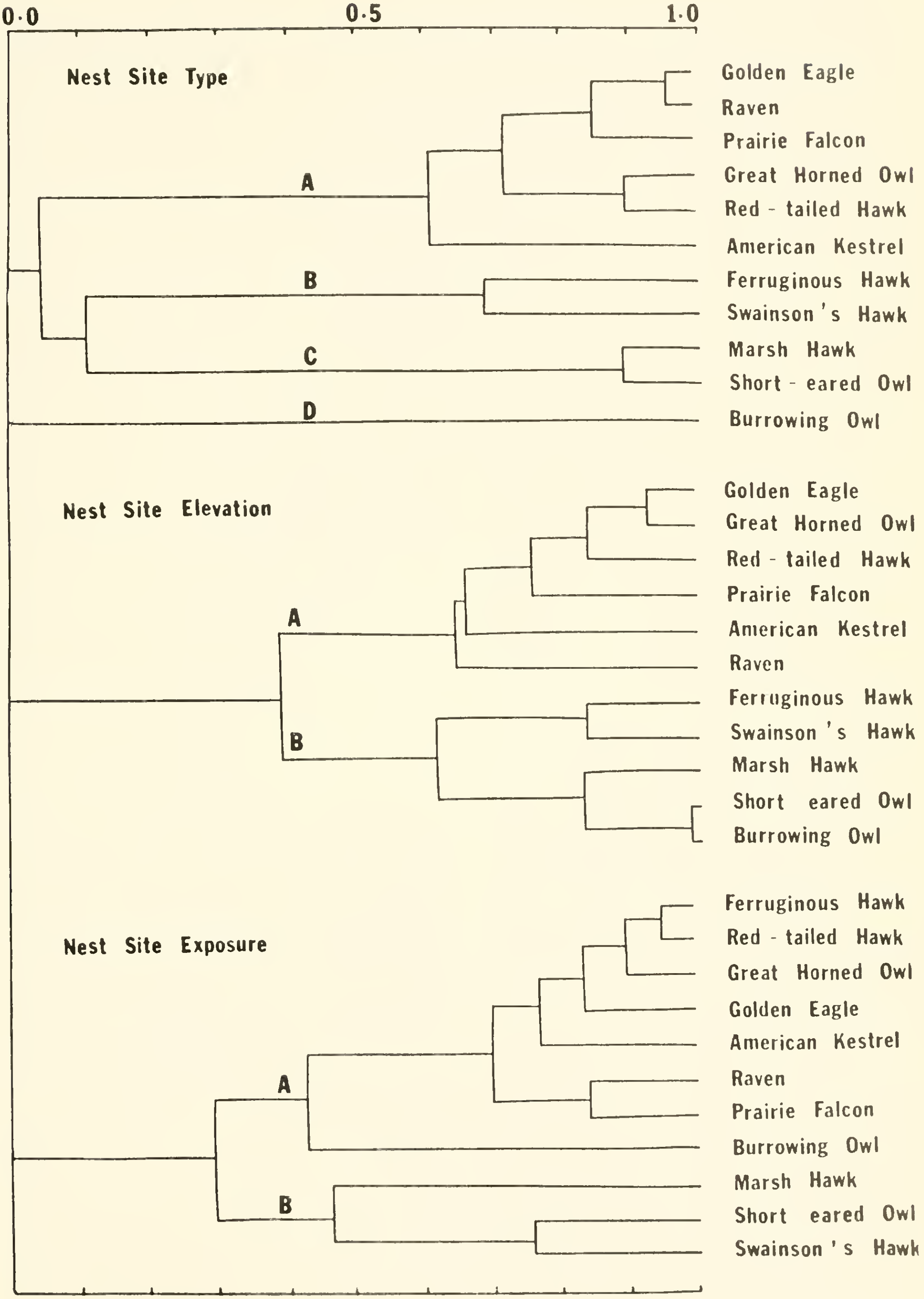


Fig. 1. Dendrograms resulting from UPGMA cluster analysis of niche overlap matrices of nest site selection dimensions among raptor species and the Raven. Separate dendrograms are constructed for each nest site resource dimension.

Swainson's Hawk combination, with the former now included in Guild A containing the other large raptor species and the latter placed in the Marsh Hawk and Short-eared Owl cluster. Two species with very similar NSX requirements are the Raven and Prairie Falcon of Guild A. Both utilize a high proportion of cavity nest sites with WNW and NNW exposure.

AVERAGE COMMUNITY OVERLAP.— Average community overlap (α) within the raptor species community was calculated for each nest site variable (Table 6). Average community overlap provides a method for broadly defining core species that characteristically show high ($\alpha > \alpha\bar{x}$) values and fringe species with low average ($\alpha < \alpha\bar{x}$) values). These α values of core species indicate high average overlap with other community raptors, whereas fringe species are more ecologically isolated.

Average community overlap may also show the degree of competitive interaction along a resource. For the raptor species community, average overlap was greatest in NSX variable ($\alpha\bar{x}$ = .5692) and least in NST ($\alpha\bar{x}$ = .2691). The lower NST and NSE overlap may suggest segregation of raptor species along these resources. The Golden Eagle again ranked high in average community overlap in all three nest site variables. Only Great Horned Owls and Red-tailed Hawks had a higher average community overlap in two nest site variables, NST and NSE, and only the Red-tailed Hawk had a higher community overlap in NSX.

There is a correlation between raptor species abundance and average community overlap, with the most common raptor species showing highest average community overlaps and qualifying as core species. This pattern is consistent with abundance correlations previously discussed. Ferruginous Hawk NST community overlap (α_T = .2213) deviates from this pattern because of its comparatively restricted choice of nest sites. Although this species used 10 of 19 NST categories, 75.5 percent of nests were located in but two categories, junipers and rock outcrops. NST and NSX average overlap (α_T = .3373; α_X = .6474) of the Raven places it among the core species, although its typical selection of nest sites at higher, more remote elevations on the study area resulted in the lowest NSE average niche overlap rank (α_E = .2102). Three raptor species have marginal rankings, the Prairie Falcon, American Kestrel, and Swainson's Hawk. The Prairie Falcon had high NST overlap (α_T = .3988) but low NSE and NSX overlap values (α_E = 3.35; α_X = .2102) and should probably be considered a marginally core member of the raptor community. Overall low average community overlaps of the Marsh Hawk, Short-eared Owl, and Burrowing Owl qualify these raptors as fringe species.

TABLE 6. Average community overlap values.[1]

Species	Nest site type	Nest site elevation	Nest site exposure
Golden Eagle	.3873 (8)	.4600 (8)	.6830 (10)
Great Horned Owl	.4632 (11)	.5453 (11)	.6758 (8)
Ferruginous Hawk	.2213 (5)	.4639 (9)	.6764 (9)
Red-tailed Hawk	.4269 (10)	.5186 (10)	.6857 (11)
Swainson's Hawk	.1604 (4)	.3548 (6)	.5318 (5)
Prairie Falcon	.3988 (9)	.3335 (2)	.4762 (4)
Marsh Hawk	.1144 (3)	.3812 (7)	.4046 (2)
American Kestrel	.2980 (6)	.3504 (5)	.6412 (6)
Short-eared Owl	.1130 (2)	.3410 (4)	.3798 (1)
Burrowing Owl	.0000 (1)	.3391 (3)	.4595 (3)
Raven	.3773 (7)	.2101 (1)	.6474 (7)
Average (all species)	.2691	.3907	.5692

[1] Figures in parentheses indicate rank.

DISCUSSION

Whittaker et al. (1973) reviewed the history and conceptual development of the terms *niche* and *habitat* as methods of describing how a species relates to the physical and biological variables within a community. They proposed that *niche* be used to describe the relationship of a species to intracommunity variables such as food size and feeding behavior, whereas *habitat* should be restricted to such spatial gradients of a community as elevation or exposure.

Nest site selection is an active process in which species respond to stimuli based on complexes of environmental variables (Fretwell 1972), although tradition and previous experience may reduce the importance of certain environmental factors (White 1969). In essence, the selection of a nest site is a behavioral response similar to the stimulus-response behaviors by which a species restricts its foraging within certain environmental constraints such as height above ground, e.g., foraging height niche of the Blue-gray Gnatcatcher (*Polioptila caerulea*) described by Root (1967). In this context, nest site selection may be considered as one axis of the n-dimensional niche hyperspace of a species.

We believe the three variables considered, type, elevation, and exposure, represent basic habitat characteristics. We assume that raptors will select some portion within each of these dimensions that collectively provide the most suitable nesting site. Raptors may, for example, choose nest site types that potentially provide such benefits as a wide platform base for rearing large broods of young (e.g., Ferruginous Hawk platform nests in tops of junipers); inaccessibility (e.g., Golden Eagle nests on high, sheer cliffs or Burrowing Owl nests in burrows), or shelter (e.g., cavity nests of Ravens and Prairie Falcons).

Nest site elevation may promote nest inaccessibility and therefore offer brood protection, provide a commanding view of the territory, or enhance lift capabilities by local updrafts resulting from uneven heating of valley floors and ridges. In this latter context selection of nesting sites at middle and higher elevations may be especially advantageous to Golden Eagles and larger hawks and owls by enabling them to forage more efficiently and return large prey to the nest.

Mosher and White (1976) elucidated the importance of directional exposure of nest site with special reference to Golden Eagles. They pointed out that exposure of young raptors to extremes of temperature and direct insolation may be a major source of thermoregulatory stress during early stages of development. Thus, raptor species will presumably tend to select nest sites with exposures that offer an optimum microclimate within reasonable variations.

Several factors are immediately evident with respect to nest site partitioning within the raptor community of this study. First, there is a significant correlation between niche breadth, average community overlap, and relative abundance of raptor species that divides the raptor community into groups of core species such as the Golden Eagle with comparatively broad niches and fringe species with narrow niches. This pattern is especially notable within guilds where it may reduce competition between species with very similar nest site requirements by restricting population size of the fringe species. Thus, along each variable we find three basic groups that correspond to raptor species that tend to nest at high, middle, and low elevations within the range of topographic habitats found in the study area. Competition within these clusters is potentially more intense compared with competition between clusters, but is reduced by two isolating mechanisms. First, raptor species of each cluster include core and fringe species. Core species common to Guild A of NST and NSE dendrograms include the Golden Eagle, Great Horned Owl, Red-tailed Hawk, and Raven. The Prairie Falcon is marginally core in this cluster, and the American Kestrel may represent a fringe species. Core and fringe species in the middle cluster are the Ferruginous Hawk and Swainson's Hawk, respectively. The three raptor species in the lower cluster rank as fringe species. Of these the Burrowing Owl is a common component of raptor communities in the eastern Great Basin desert.

Wiens (1977) noted that competition theory predicts that other species may successfully invade communities during periods of high resource availability. In this context the presence and abundance of fringe species may be a function of food supply available to the core species. Core species such as the Golden Eagle increase territory size when their prey base is low and reduce average territory size when their prey base is high (Smith and Murphy 1973, 1979). This reduction may collectively be sufficient to allow invasion by fringe species. Conversely, in low prey years core species compensate by increasing territorial size and may thereby exclude such fringe species.

A second factor that reduces competition within clusters is different time-activity patterns. This mechanism separates the nocturnal Great Horned Owl from two diurnal raptor species with very similar nest site requirements, the Red-tailed Hawk and Golden Eagle. A parallel isolation is also evident within the Marsh Hawk and Short-eared Owl guild. The crepuscular activity of the Ferruginous Hawk at least partially isolates it from the more diurnal Swainson's Hawk.

In summary, raptor species partition nest sites along the three environmental variables examined, although several within cluster species show comparatively broad overlap. At least part of this overlap may be attributed to niche hyperspace differences not examined in this study, such as foraging area, prey selection, and breeding chronology.

The nest site relationships and structure of the raptor community are a measure of intra- and interspecific raptor species populations adapting to habitats of the eastern Great Basin desert and should not be construed as levels of general adaptability or relationships equally applicable in all habitats.

Acknowledgments

This study was partially funded by a NDEA Title IV predoctoral fellowship awarded to the senior author. We thank Clayton M. White, Carl D. Marti, and Donald A. McCrimmon, Jr., for their valuable criticisms of earlier drafts of the manuscript.

Literature Cited

Cody, M. L. 1974. Competition and the structure of bird communities. Mongr. Popul. Biol. No. 7. Princeton Univ. Press, Princeton, New Jersey. 318 pp.

Culver, D. A. 1972. A niche analysis of Colorado ants. Ecology 53:126–131.

Fretwell, S. D. 1972. Populations in a seasonal environment. Mongr. Popul. Biol. No. 5. Princeton Univ. Press, Princeton, New Jersey. 217 pp.

Horn, H. S. 1966. The measurement of overlap in comparative ecological studies. Am. Nat. 100:419–424.

Lack, D. A. 1946. Competition for foods by birds of prey. J. Anim. Ecol. 15:123–129.

Levins, R. 1968. Evolution in changing environments. Princeton Univ. Press. Princeton, New Jersey. 120 pp.

McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. Science 167:131–138.

Mosher, J. A., and C. M. White. 1976. Directional exposure of Golden Eagle nests. Canad. Field Nat. 90:356–459.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37:317–350.

Shelford, V. E. 1963. The ecology of North America. Univ. of Illinois Press. Urbana, Illinois. 610 pp.

Smith, D. G., and J. R. Murphy. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. BYU Sci. Bull., Biol. Ser. 18(3):1–76.

Smith, D. G., and J. R. Murphy. 1979. Breeding responses of raptors to jackrabbit density in the eastern Great Basin desert of Utah. Raptor Research 13:1–14.

Smith, D. G., J. R. Murphy, and N. Woffinden. 1981. Relationships between jackrabbit abundance and Ferruginous Hawk reproduction. Condor 83:52–56.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco. 359 pp.

White, C. M. 1969. Is there a genetic continuity concerned in eyrie maintenance? Pages 381–398 *in* J. J. Hickey, ed., Peregrine Falcon populations: their biology and decline. Univ. of Wisconsin Press. Madison, Wisconsin. 596 pp.

Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. Niche, habitat, and ecotype. Amer. Natur. 107:321–338.

Wiens, J. A. 1977. On competition and variable environments. Am. Sci. 65:590–597.

INVERTEBRATE FAUNAS AND ZOOGEOGRAPHIC SIGNIFICANCE OF LAVA TUBE CAVES OF ARIZONA AND NEW MEXICO

Stewart B. Peck[1]

Abstract.— A field survey in caves near Grants, New Mexico, and Flagstaff, Arizona, found only an exceptionally poor fauna of 14 species with no strong patterns of cave restriction. The faunal poverty is judged to be correlated with and influenced by the similarly impoverished boreal forests in nearby mountains. Species of flightless arthropods, suitable for cave colonization and restricted to cool-moist litter of boreal ("Hudsonian-Canadian Life Zone") forests, are apparently not now present in suitable, nearby mountain habitats. They may not have dispersed to all available montane sites from the Southern Rocky Mountains during glacial conditions. Either the forests did not exist as continuous dispersal corridors for the litter arthropods, or the fauna could not track the rate of spread of the forests.

The lava tube caves of the Colorado Plateau of New Mexico and Arizona (Fig. 1) are still inadequately explored. Lava tubes elsewhere, such as in the Pacific Northwest, Japan, Hawaii, and the Galapagos (Peck 1973, Howarth 1973), contain a very distinctive fauna. It is therefore possible that a specialized fauna exists in some of the lava tube caves of the Colorado Plateau.

The reasoning is based on previous work in some "Canadian-Hudsonian Life Zone" forests in the mountains of the southwest indicating an unsuspected diversity of invertebrates similar to those in caves (Peck 1978, 1980). The strongest hypothesis accounting for most of the elements in the temperate terrestrial cave faunal assemblage suggests they were derived from preadapted (montane) mesic forest litter inhabitants. These species probably encountered lower elevation and lower latitude caves during glacials (pluvials) when appropriate forest "life zones" occurred at lower elevations and latitudes. These populations were then isolated in caves during interglacials (interpluvials) (Barr 1967, 1968), survived in them, and presumably underwent population evolution.

Two areas in the southwestern United States contain lava tube caves that seem to ideally fit the prerequisites of faunal establishment and evolution. Field workers in July and August of 1975, 1977, and 1979 surveyed these lava tube caves near Grants, New Mexico, and Flagstaff, Arizona, and also examined many montane litter populations.

Field Sites

New Mexico.— A large volcanic field occurs near Grants, New Mexico (Thornbury 1965, Hunt 1956, 1974). The Bandera Lava Field, or Grants Malpais, contains numerous and extensive lava tubes (Hatheway 1977) at the foot of the Zuni Mountains (9100 ft elevation) and Mount Taylor (11,300 ft), a central-type volcano. The lava field biota is discussed by Lindsay (1951). The main lava flow is of late Pleistocene age and covers about 220 square miles, from about 8300 ft down to 6200 ft. The caves, occurring in habitats of Transition down to Upper Sonoran Life Zones (Fig. 2), are indicated on the Ice Caves 7.5 minute topographic quadrangle of the U.S. Geological Survey.

Many sites were sampled: Ice Caves, and six other cave-sink segments of the same cave system in Secs. 22, 23, and 26, T9N, R11W, on the continental divide at approximately 7800 ft; eight cave sections and sinks on the northern slope of Lava Crater, Sec. 25, T9N, R11W, at approximately 7800 ft; and eight cave segments and sinks in Sec. 33, T9N, R11W, including Truckett Guano Cave (Bat Cave), at about 7300 ft. The caves were judged, based on other comparable caves, to

---

[1] Department of Biology, Carleton University, Ottawa, Ontario, K1S, 5B6, Canada.

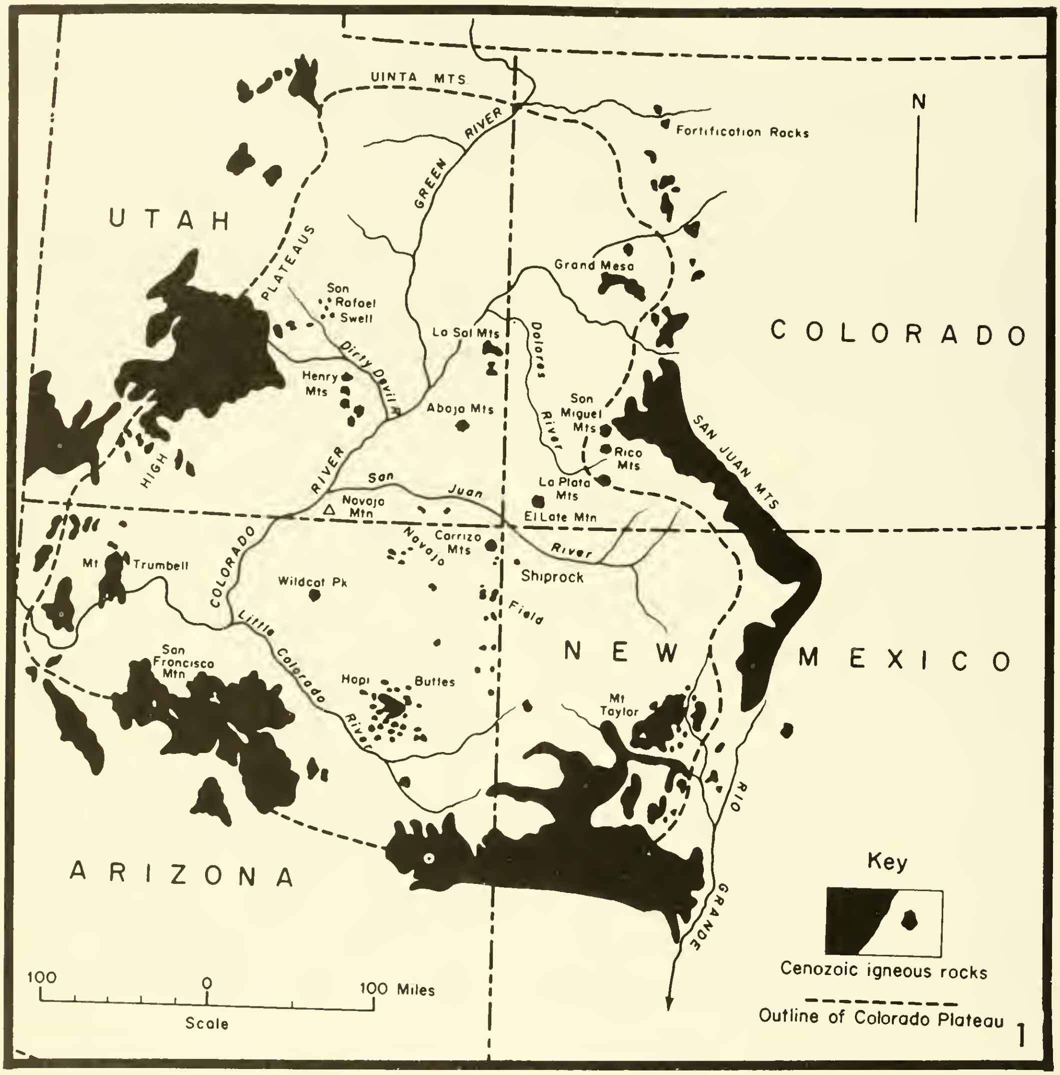

UINTA MTS
N
Fortification Rocks
GREEN RIVER
UTAH
HIGH PLATEAUS
Grand Mesa
COLORADO
San Rafael Swell
La Sal Mts
Dolores River
Dirty Devil
Henry Mts
Abajo Mts
San Miguel Mts
SAN JUAN MTS
Rico Mts
RIVER
San Juan River
La Plata Mts
Navajo Mtn
El Late Mtn
Carrizo Mts
Navajo Field
Mt Trumbell
COLORADO
Shiprock
Wildcat Pk
NEW MEXICO
San Francisco Mtn
Little Colorado River
Hopi Buttes
Mt Taylor
RIO GRANDE
ARIZONA
Key
Cenozoic igneous rocks
Outline of Colorado Plateau
100
0
100 Miles
Scale
1

Fig. 1. Map showing distribution of Cenozoic igneous rocks on the Colorado Plateau. Pleistocene and Recent basalt lava flows with lava tubes are most common near Mount Taylor, New Mexico, and the San Francisco Mountains, Arizona (after Hunt 1974).

be suitable for invertebrates. Seemingly adequate food inputs, extensive dark zones, abundant moisture, and cool to cold temperatures (several have permanent ice) also supported the supposition. Only Truckett Guano Cave (with multiple entrances at different elevations and associated continuous air currents) is too warm and dry to contain cave-restricted faunas.

Additional litter surveys were made in epigean habitats of cool, moist, forested, talus slopes on Lava Crater and on Mount Taylor at elevations of 8500, 9000, 10,500 and 11,000 ft, as well as in the Guadelupe, Sierra Blanca, Manzano, Sandia, Santa Fe, Sangre de Cristo, and Magdalena ranges.

Arizona.— The San Francisco Volcanic Field, near Flagstaff, covers about 3000 square miles and is the second largest in the contiguous United States (Hunt 1956, 1974, Robinson 1913, Thornbury 1956). The oldest flows are 6.2 ± 1.2 million years by K-Ar dating (Colton 1967). The field is topped by Humphreys Peak (12,680 ft), which experienced extensive Pleistocene glaciation (Péwé and Updike 1976, Sharp 1942).

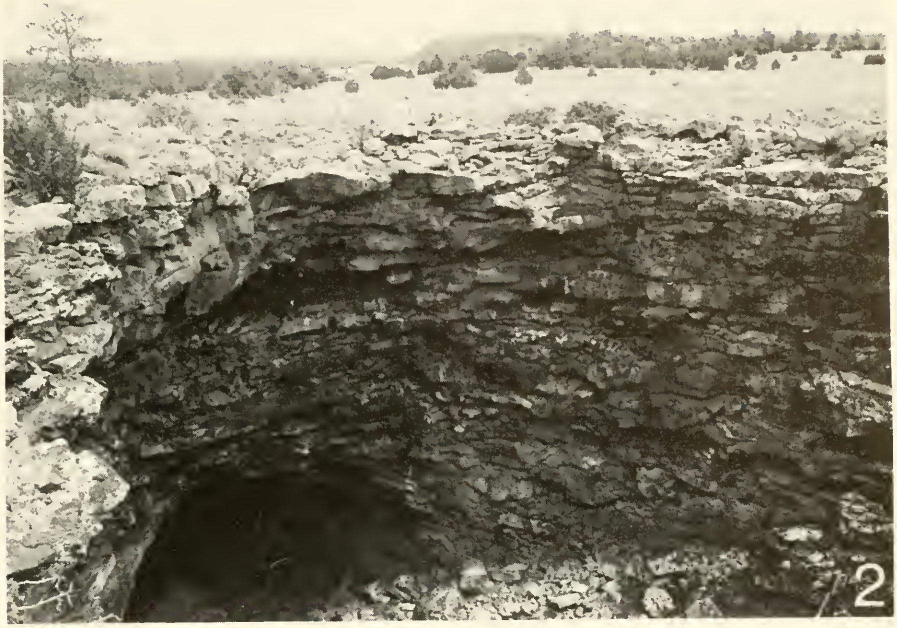


Fig. 2. Sink entrance to segment of lava tube system near Truckett Guano Cave, near Ice Caves, New Mexico, at 7300 ft elevation, in a pinyon-juniper-grassland community. During full glacial climatic conditions the area may have been covered by a boreal forest of spruce and fir.

The caves lie in extensive sheets of third-period eruptive basaltic lava (late Pleistocene to Recent). These sheets cover about 1200 square miles and are situated in a ponderosa pine-grassland (Transition Life Zone) at about 7000 ft (Fig. 3). The environmentally varied caves are described by Forney (1971), Hassemer (1962), and Ingold (1964). I found the following: Slate Lakes Cave had a temperature of 7 C. Kana-a Cave is too small, close to the surface, and warm (15 C) to contain a significant fauna. Sunset Crater Ice Cave, with permanent ice (air temp 1 C) and abundant organic matter, is heavily visited by tourists to Sunset Crater National Monument. Lava River Cave, also called Government Cave, is the largest, with about 3600 feet of passage. It seems well suited to contain a cave fauna. Some ice was present near the entrance talus slope, and the air temperature was 4 C and the relative humidity 94 percent 1000 feet inside. At the cave end the air temperature was 6 C and the relative humidity was 97 percent. Scattered thin accumulations of bat guano yielded no fauna in Berlese extraction nor did pack-rat fecal piles. Porcupine fecal piles are abundant and extensive, but, again, Berlese extraction yielded no fauna. Numerous small cheese and carrion baits along the length of the cave yielded no fauna in either 1977 or 1979. Lange (1956) found the remains of woodchucks (*Marmota flaventris*) in Lava River Cave. This species presently occurs no nearer than Kane County, Utah, across the Colorado River. This represents a postglacial regional extinction.

Mountain litter was sampled for fauna on Humphreys Peak, the Chuska Mountains, Mogollon Rim and the White Mountains, and the Kaibab Plateau.

Annotated Faunal List

Some New Mexican cave faunas are reported in Welbourne (1978), who is also preparing a report on the cave faunas of the limestone caves of New Mexico. The only Arizona caves to be fully surveyed for invertebrates are in the Grand Canyon (Peck 1980). In many of the collections reported below, species level determinations are not now possible. The following contains the standard terminology for cavernicolous animals (Barr 1968): troglobitic is obligately cavernicolous; troglophilic is facultatively cavernicolous.

Phylum Arthropoda

Class Arachnida

Order Acarina

Family Rhagidiidae

Undetermined genus and species. One specimen from Truckett Guano Cave. These are often found in cool and wet situations in forests and caves. Most species are troglophiles and have very wide ranges, but two troglobitic genera occur in Idaho and Washington (Elliott 1976, Zacharda 1981).

Family undetermined; mites in three families occur in guano in Truckett Guano Cave. These are currently under study by W. C. Welbourne.

Order Pseudoscorpionida

Undetermined species (immatures, possibly *Dinocheirus astutus* Hoff, Chernetidae); collected from sinkhole debris of a cave near Ice Caves. Commonly present in bat guano in Truckett Guano Cave.

Class Diplopoda

Order Julida

Family Nemasomidae

"Nemasoma" uta Chamberlin, W. Shear det. One specimen in caves near Ice Caves. Although certain species of millipeds are frequent cave inhabitants, this species is considered accidental.

Class Collembola

Order Entomobryomorpha

Family Entomobryidae

Tomocerus flavescens (Tullberg), K. Christiansen det. Several specimens were taken in caves near Ice Caves. The species is widespread across most of North America and is a common cave inhabitant (Christiansen 1964, Christiansen and Bellinger 1980).

Class Insecta

Order Diplura

Family Campodeidae

Metriocampa sp., L. Ferguson det. Four specimens of this troglophilic species were found in litter in caves near Ice Caves and in sink debris near Lava Crater. These are widespread soil inhabitants and are occasionally found in caves. Some species are troglobitic. Some generic distributions show east-west disjunctions.

Order Orthoptera

Family Rhaphidophoridae

Ceuthophilus sp. A few immature individuals were found in Truckett Guano Cave, Kana-a Cave, and Ice Cave. The genus is a common trogloxenic inhabitant of caves, which are used as daytime refuges or as hibernacula.

Order Coleoptera

Family Staphylinidae

Atheta sp. Several specimens were in moist litter in Truckett Guano Cave. This commonly troglophilic genus is often found in caves, but the species are wide ranging.

Family Lathridiidae

Enicmus sp. One specimen was taken from pack-rat dung in Slate Lake Cave entrance talus. These are scavengers on fungi and are often in decaying and moldy materials.

Order Siphonaptera

Undetermined fleas (possibly *Sternopsylla texana* [Fox]) were extremely abundant in guano in Truckett Guano Cave.

Order Diptera

Family Mycetophilidae

Mycetophila fungorum (DeGeer), R. Vockeroth det. Seven specimens were captured from the ceiling near the entrance of Slate Lake Cave. The species is widespread from Quebec to Alaska and south to Mexico.

Family Sphaeroceridae

Leptocera sp. A few specimens were in Truckett Guano Cave. These flies are commonly scavengers in caves and forest litter.

Family Ephydridae

A few undetermined specimens were found in Truckett Guano Cave. Flies in this family are occasionally scavengers on guano.

Discussion

The caves were initially judged to have good potential for harboring a community of cavernicolous invertebrates. Lava tubes in Oregon, Washington, and Idaho have a rich and highly evolved cave fauna, and a cave-evolved fauna exists in caves near the bottom of the nearby Grand Canyon (Peck 1973, 1980). Although the caves were found to appear to be environmentally suitable, how-

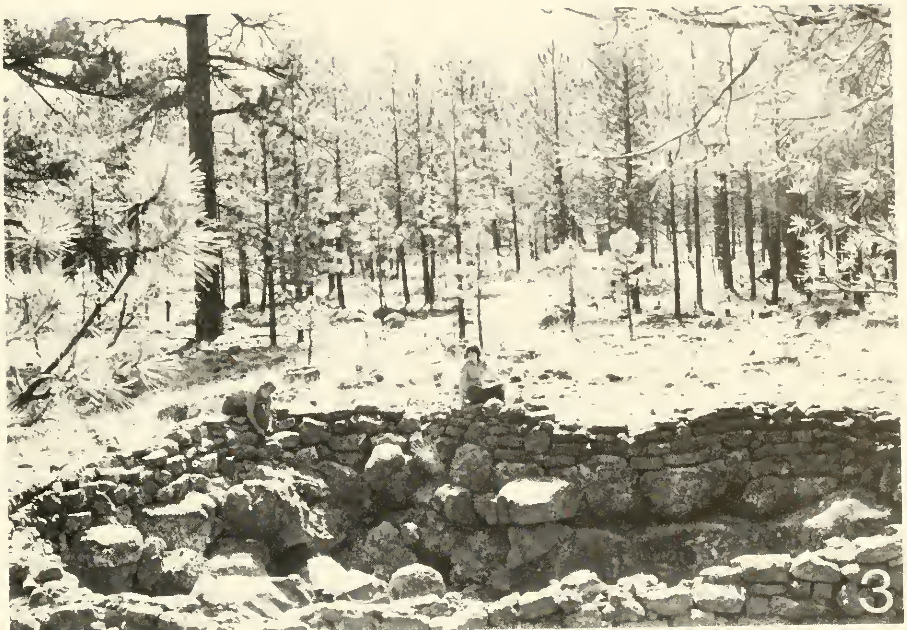


Fig. 3. Sink entrance to Lava River Cave, NW of Flagstaff at 7700 ft elevation, in a ponderosa pine parkland. During full glacial conditions the region may have been covered by a boreal forest of spruce and fir, but a diverse litter fauna may not have been present to occupy the subterranean habitats of the lava flows.

ever, the fauna was exceedingly impoverished and contained solely species that have peripheral ecological associations with caves. This raises the problem of explaining the lack of a fauna.

A number of possible reasons are suggested and discussed. These are: (1) Inadequate field work. This seems unlikely because of the number of sites visited, the time spent in searching, and the variety of sampling techniques used that have been productive elsewhere. Future work in the caves can test this supposition. (2) Present environmental unsuitability. This seems unlikely, judging from inspection of the habitats. No differences in the lava tube caves between the survey areas and those of the Pacific Northwest, with a rich fauna, are apparent. (3) Past environmental unsuitability of the caves. The caves, some now containing permanent ice, may have been even colder, more ice filled, and uninhabitable during the changed climates of the glacials (pluvials). If so, earlier occupations may have been pushed to extinction, so that only modern colonists are present. Periglacial climatic unsuitability of caves at certain times has been suggested for Illinois (Peck and Lewis 1977), Canada (Peck and Fenton 1977), and the Uinta Mountains of Utah (Peck 1981). Nevertheless, the presence of the well-developed cave faunas in Idaho and Washington, which also experienced equal or greater glacial rigors, does not support this idea. (4) Inadequate age of the caves. This is unlikely. All specialized lava tube faunas exist in caves of mid- and late Pleistocene age, and of even Recent age. It is obvious that the faunas have used the abundant cracks and crevices of the basalt flows to continually move into progressively younger caves (Howarth 1973). (5) Inadequate climatic change as a stimulus for biotic movement. This must be rejected. Abundant data on biotic elevational and latitudinal shifts are available (reviewed in Martin and Mehringer 1965, Van Devender and Spaulding 1979, Wells 1979). Pollen from lake cores (Whiteside 1965) and packrat midden analyses (Van Devender and Spaulding 1979) are but two analytical methods of documenting this in the southwest. (6) The absence of a suitable ancestral litter fauna. This seems the most likely remaining cause for a lack of cavernicolous species and is supported by my empirical field observations. The diverse, rich, and balanced fauna of many taxa of flightless litter arthropods, composed of harvestmen, spiders, pseudoscorpions, millipeds, mites, diplurans, camel crickets, beetles, etc., of many southwestern montane forests seems to be impoverished or has many taxa missing on Mount Taylor and the San Francisco Mountains. Quantitative field survey work in spring and fall field seasons (more appropriate for litter faunas than my midsummer sampling) can test this impression. Data are now too few to otherwise test this idea. The only distributional analysis of southwestern forest litter vertebrates is that of pseudoscorpions by Hoff (1959). The lack of epigean survivors of close ancestors of the rich invertebrate fauna of Texas caves (Mitchell and Reddell 1971) might seem to argue against this observation. The mesic forest connections of the past from central Texas to the southeastern United States, however, are well documented (Martin and Harrell 1957), and the present aridity must be considered to be too intense to have allowed epigean survival of most ancestral stocks in the cavernous regions of central Texas.

If the lack of litter-inhabiting ancestors is real, then there are interesting implications. These are based on the assumption that the now-disjunct distributions of many taxa of flightless forest-litter arthropods with narrow ecological preferences or tolerances are indicators of past forest connections or continuity (discussed in Lawrence 1953). My preliminary findings are that present-day litter arthropod distributions indicate that continuous boreal forests, suitable as dispersal avenues during full glacials (pluvials), existed from the southern Rocky Mountains of Colorado down both sides of the Rio Grande depression to at least Sierra Blanca and the Magdalena Mountains. Mount Taylor should have been on this corridor, but the lack of many litter invertebrates suggest that it wasn't.

The San Francisco Mountains of Arizona are isolated from the Kaibab Plateau and other forest faunal source areas in the north by the Grand Canyon and lowlands of the Colorado, Little Colorado, and San Juan rivers. Nevertheless they too should have been connected by the highlands of the Mogollon Rim and White Mountains through the Datil Section to the mountains (including Mount Taylor) on the west side of the Rio Grande in New Mexico.

Problems of water loss from cuticular abrasion in volcanic soils can severely restrict the diversity of arthropods that can live in it (Edwards and Schwartz 1981). I have not subjectively noticed this in the soil and litter faunas of many volcanic areas in which I have worked, however. Also, both volcanoes (but not their basal vents and flows) have been inactive since the mid-Pleistocene, and more than enough time has since elapsed for subsequent faunal and floral occupation.

The poorer faunas of Mount Taylor and the San Francisco Mountains may be indicators that there have been persistent and significant barriers between them and the more northerly faunal source areas. Present-day southwestern boreal forests are discontinuous in distribution. This is caused by intervening lowland regions with unsuitable temperatures and inadequate rainfall. Past glacial-pluvial temperatures and rainfall in the southwest are known to have been suitable for more widespread coverage by woodlands and other forest types at lower elevations than at present (Van Devender and Spaulding 1979, Wells 1979). The boreal forests were probably not all in continuous contact (in contrast to Martin and Mehringer 1965), however. The gaps may have been more easily crossed by boreal-forest plants than by litter invertebrates with lower dispersal abilities. Thus, the plants may have spread farther and faster than the invertebrates. For instance, long-distance dispersal (probably of seeds) has allowed an impoverished and disjunct boreal and tundra flora to reach the San Francisco Peaks (Moore 1965).

In conclusion, further survey work of the taxa and distribution of montane forest litter and cave-inhabiting invertebrates of the San Francisco Mountains, Zuni Mountains, Mount Taylor, and others may contribute to understanding questions of cave colonization. More importantly, they should contribute to more general questions of Pleistocene biogeography and the historical dynamics of the still poorly understood boreal forest "communities" of the southwest (see Harper and Reveal 1978).

ACKNOWLEDGMENTS

Hana Kukal, Olga Kukal, Morag McPherson, and Jarmila Peck helped with the collecting in caves and mountain forests, thereby greatly increasing the efficiency and accuracy of the faunal surveys. Gerald G. Forney and Glenda Rhodes provided information on cave locations. Arthur M. Phillips III provided data on montane floras and Pleistocene vegetational changes. The Museum of Northern Arizona, Flagstaff, provided space for a field camp and Berlese extractions of litter samples. The manuscript was read by Andy Grubbs, William R. Elliott, Peter Price, Paul S. Martin, and three anonymous reviewers. Field support was from operating grants of the Canadian Natural Sciences and Engineering Research Council for work on the systematics and distribution of cave and litter faunas.

LITERATURE CITED

BARR, T. C., JR. 1967. Observations on the ecology of caves. Amer. Natur. 101:475–492.

_____. 1968. Cave ecology and the evolution of troglobites. Evol. Biol. 2:35–102.

CHRISTIANSEN, K. 1964. A revision of the Nearctic members of the genus *Tomocerus* (Collembola Entomobryidae). Rev. Eco. Biol. Sol. 1:639–678.

CHRISTIANSEN, K., AND P. BELLINGER. 1980. The Collembola of North America, north of the Rio Grande. Part 3, Family Entomobryidae. Grinnel College, Grinnel, Iowa.

COLTON, H. S. 1967. Basaltic cinder cones and lava flows of the San Francisco Mountain Volcanic Field. Mus. Northern Arizona Bull. 10 (rev. ed.), 58 pp.

EDWARDS, J. S., AND L. M. SCHWARTZ. 1981. Mount St. Helens ash: a natural insecticide. Canadian J. Zool., 59:714–715.

ELLIOTT, W. R. 1976. New cavernicolous Rhagidiidae from Idaho, Washington, and Utah (Prostigmata: Acari: Arachnida). Occ. Pap. Mus. Texas Tech. Univ. 43:1–15.

FORNEY, G. G. 1971. Lava tubes of the San Francisco volcanic field, Arizona. Plateau (Mus. Northern Ariz.). 44:1–13.

HARPER, K. T., AND J. L. REVEAL, eds. 1978. Intermontane biogeography: a symposium. Great Basin Nat. Mem. No. 2. 268 pp.

HASSEMER, J. 1962. Basalt cave (Coconio County, Arizona). Speleo Digest 1962:1-7–1-8 and map.

HATHEWAY, A. W. 1977. Lava tube formation, the makings of a controversy; Findings from studies on the Bandera Lava Field, New Mexico. Pages 11–18 *in* W. R. Halliday, ed., Proc. Int. Symp. vulcanospeleology and its extraterrestrial applications. Spec. Pub. Western Speleological Survey, Seattle, Washington. 85 pp.

HOFF, C. C. 1958. The ecology and distribution of the pseudoscorpions of north central New Mexico. Univ. of New Mexico Publ. Biol. No. 8. Univ. of New Mexico Press, Albuquerque. 68 pp.

HOWARTH, F. G. 1973. The cavernicolous fauna of Hawaiian lava tubes, I. Introduction. Pacific Insects 15:139–151.

HUNT, C. B. 1956. Cenozoic geology of the Colorado Plateau. U.S. Geol. Surv. Prof. Pap. 279. 99 pp.

_____. 1974. Natural regions of the United States and Canada. W. H. Freeman and Co., San Francisco. 725 pp.

INGOLD, N. 1964. Government Cave (Bellemont, Arizona). Speleo Digest 1964:1-107–1-109.

LANGE, A. L. 1956. Woodchuck remains in northern Arizona caves. J. Mammal. 37:289–291.

LAWRENCE, R. F. 1953. The biology of the cryptic fauna of forests. A. A. Balkema, Cape Town. 408 pp.

LINDSEY, A. A. 1951. Vegetation and habitats in a southwestern volcanic area. Ecol. Monog. 21:227–253.

MARTIN, P. S., AND B. E. HARRELL. 1957. The Pleistocene history of temperate biotas in Mexico and eastern United States. Ecology 38:468–480.

MARTIN, P. S., AND P. J. MEHRINGER, JR. 1965. Pleistocene pollen analysis and biogeography of the southwest. Pages 433–450 *in* H. E. Wright, Jr., and D. G. Frey, eds., The Quaternary of the United States, Princeton Univ. Press, Princeton. 922 pp.

MITCHELL, R. W., AND J. R. REDDELL. 1971. The invertebrate fauna of Texas caves. Pages 35–90 *in* E. L. Lundelius and B. H. Slaughter, eds., Natural history of Texas caves. Gulf Natural History Pubs., Dallas. 174 pp.

MOORE, T. C. 1965. Origin and disjunction of the alpine tundra flora on San Francisco Mountain, Arizona. Ecology 46:860–864.

PECK, S. B. 1973. A review of the invertebrate fauna of volcanic caves in western North America. Natl. Speleol. Soc. Bull. 35:99–107.

_____. 1978. New montane *Ptomaphagus* beetles from New Mexico and zoogeography of southwestern caves (Coleoptera: Leiodidae; Catopinae). Southwest. Natur., 23:227–238.

_____. 1980. Climatic changes and the evolution of cave invertebrates in the Grand Canyon, Arizona. Natl. Speleol. Soc. Bull. 42:53–60.

_____. 1981. The invertebrate fauna of the caves in the Uinta Mountains, northeastern Utah. Great Basin Nat. 41:207–212.

PECK, S. B., AND M. B. FENTON. 1977. The fauna of Canadian caves. Proc. 6th Int. Cong. Speleol., V, sub-sect. Db, pp. 195–200. Academia, Praha.

PECK, S. B., AND J. J. LEWIS. 1978. Zoogeography and evolution of the subterranean invertebrate faunas of Illinois and southeastern Missouri. Natl. Speleol. Soc. Bull. 40:39–63.

PÉWÉ, T. L., AND R. G. UPDIKE. 1976. Geological history of the San Francisco Peaks, with emphasis on the glacial record. Pages 16–32 *in* T. L. Péwé and R. G. Updike, eds., San Francisco Peaks: a guidebook to the geology. 2d ed., Museum of Northern Arizona, Flagstaff. 80 pp.

Robinson, H. H. 1913. The San Francisco Volcanic Field, Arizona. U.S. Geol. Surv. Prof. Pap. 76. 213 pp.

Sharp, R. P. 1942. Multiple Pleistocene glaciation in San Francisco Mountains, Arizona. J. Geol. 50:481–503.

Thornbury, W. D. 1965. Regional geomorphology of the United States. John Wiley and Sons, New York. 609 pp.

Van Devender, T. R., and W. G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. Science 204:701–710.

1,0 Welbourne, W. C. 1978. Biology of Ogle Cave with a list of the cave fauna of Slaughter Canyon. Natl. Speleol. Soc. Bull. 40:27–34.

Wells, P. V. 1979. An equable glaciopluvial in the West: pleniglacial evidence of increased precipitation on a gradient from the Great Basin to the Sonarian and Chihuahuan deserts. Quat. Res. 12:311–325.

Whiteside, M. C. 1965. Paleoecological studies of Potato Lake and its environs. Ecology 46:807–816.

Zacharda, M. 1981. Soil mites of the family Rhagidiidae (Actinedida: Eupodoidea). Morphology, systematics, ecology. Acta Univ. Carolinae: Biologica (Prague). 1978:489–785.

ADDITIONS TO THE VASCULAR FLORA OF MONTANA AND WYOMING

Robert W. Lichvar[1] and Robert D. Dorn[2]

Abstract.— A list of one taxon new for Montana and 10 new for Wyoming is presented, plus comments about *Astragalus molybdenus.*

Recent field work has added one additional species to the flora of Montana and 10 additional species for Wyoming. The following herbaria were consulted for the taxa reported below: BYU, COLO, CSU, ID, IDS, MONT, MONTU, NEB, RM, US, UTC. Comments on the taxonomic status of *Astragalus molybdenus* Barneby in Wyoming are included.

Asteraceae

Ratibida tagetes **(James) Barnh.** Wyoming, Laramie Co., 3 miles W. of Cheyenne (T14N R67W S28 SE¼ SW¼), 1890 m, 17 Aug 1980, *R. Dorn 3612,* RM.

First report for Wyoming. Likely introduced with Blue Grama seed.

Solidago speciosa **Nutt.** Wyoming, Crook Co., Bear Lodge Mountains (T54N R62W S20), 1430 m, 18 July 1980, *R. Lichvar 3185,* RM; *R. Dorn 3545,* RM.

First report for Wyoming. In Atlas Fl. Gt. Plains (Barkley 1977) a dot is given for Goshen Co., but that dot represents a specimen of S. *missouriensis* (R. Hartman, pers. comm., 1981).

Brassicaceae

Draba verna **L.** Wyoming, Yellowstone National Park, Old Faithful area near Belgian Pool, 2285 m, 25 Apr 1980, *R. Lichvar 2544,* RM.

First report for Wyoming.

Campanulaceae

Campanula aparinoides **Pursh.** Wyoming, Crook Co., Bear Lodge Mountains (T54N R63W S2), 1430 m, 18 Jul 1980, *R. Dorn 3549,* RM, US; *R. Lichvar 3196,* RM, US.

First report for Wyoming.

Crossosomataceae

Forsellesia meionandra **(Koehne) Heller.** Wyoming, Sweetwater Co., Little Firehole Basin (T17N R106W S26 NW¼ NW¼), 2040 m, 2 Jul 1980, *R. Dorn 3508,* RM. Sweetwater Co. (T16N R106W S10 SE¼), 1980 m, 3 Jul 1980, *R. Dorn 3512,* RM.

First report for Wyoming.

Cyperaceae

Carex granularis **Muhl.** Wyoming, Crook Co., Bear Lodge Mountains (T54N R63W S2), 1430 m, 18 Jul 1980, *R. Lichvar 3206,* RM; *R. Dorn 3548,* RM.

First report for Wyoming.

Fabaceae

Astragalus molybdenus **Barneby.** Wyoming, Lincoln Co., Salt River Range, Head of Corral Creek (T31N R117W S16), 2865 m, 21 Aug 1980, *R. Dorn 3661,* RM, NY; *R. Lichvar 3600,* RM, NY. Same location, 17 Sept 1980, *R. Lichvar 3926,* RM, NY; *R. Dorn 3682,* RM, NY.

The Sept collections represent the first collection of fruits for this species in Wyoming. Barneby (1964) noted "An astragalus resembling *A. molybdenus* in habit . . . collected in flower in the Salt River Mountains in Western Wyoming . . ." and commented that, "when better known may prove to be a second member of sect. *Minerales*." We cannot distinguish the flowering and fruiting material of the Wyoming material from the Colorado material of *A. molybdenus*. Barneby (1980) has described this as a new species, *A. shultziorum*.

---

[1] Wyoming Natural Heritage Program, The Nature Conservancy, 1603 Capitol Avenue, No. 325, Cheyenne, Wyoming 82001.

[2] P.O. Box 1471, Cheyenne, Wyoming 82001.

Oxytropis riparia **Litv.** Wyoming, Fremont Co., Ice Slough along Rt. 287 (T29N R93W S6 NW¼), 2285 m, 11 Aug 1980, *R. Lichvar 3407*, RM.

Second report for Wyoming. S. Welsh (pers. comm., 1979) reported a collection from Seedskadee Natl. Wildlife Refuge, Sweetwater Co., but no specimens have been seen.

LABIATAE

Lycopus uniflorus **Michx.** Wyoming, Crook Co., Bear Lodge Mountains (T54N R63W S11 N½), 1433 m, 5 Sept 1981, *R. Dorn 3718*, RM, NY.

First report for Wyoming.

POACEAE

Phippsia algida **(Phipps) R. Br.** Montana, Carbon Co., Beartooth Plateau (T9S R19E S33 NW¼), 2990 m, 12 Aug 1980, *R. Dorn 3586*, RM, MONT.

First report for Montana.

POTAMOGETONACEAE

Potamogeton crispus **L.** Wyoming, Sweetwater Co., Flaming Gorge (T14N R108W S13 SW¼), 1830 m, 24 Sept 1979, *D. Shute s.n.*, RM; Sweetwater Co., Flaming Gorge at Utah-Wyoming state line (T12N R108W S20 NE¼), 1830 m, 1 July 1980, *R. Lichvar, 2880*, RM.

First report for Wyoming.

RANUNCULACEAE

Anemone virginiana **L.** Wyoming, Crook Co., Bear Lodge Mountains, (T54N R63W S2), 1430 m, 18 Jul 1980, *R. Dorn 3550*, RM.

First report for Wyoming.

LITERATURE CITED

BARKLEY, T. M., ed. 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press, Ames. 600 pp.

BARNEBY, R. 1964. Atlas of North American *Astragalus*. Memoirs of the New York Botanical Garden Vol. 13.

———. 1980. Dragma Hippomanicum VII. A New Alpine *Astragalus* (Leguminosae) from western Wyoming. Brittonia 33(2):156–158.

NOTICE TO CONTRIBUTORS

Manuscripts intended for publication in the *Great Basin Naturalist* or *Great Basin Naturalist Memoirs* must meet the criteria outlined in paragraph one on the inside front cover. They should be directed to Brigham Young University, Stephen L. Wood, Editor, Great Basin Naturalist, 290 Life Science Museum, Provo, Utah 84602. Three copies of the manuscript are required. They should be typewritten, double spaced throughout on one side of the paper, with margins of at least one inch on all sides. Use a recent issue of either journal as a format, and the *Council of Biology Editors Style Manual, Fourth Edition* (AIBS 1978) in preparing the manuscript. An abstract, about 3 percent as long as the text, but not exceeding 200 words, written in accordance with *Biological Abstracts* guidelines, should precede the introductory paragraph of each article.

All manuscripts receive a critical peer review by specialists in the subject area of the manuscript under consideration. Authors may recommend one or two reviewers for their article.

Accepted manuscripts less than 100 printed pages in length will automatically be assigned to the *Great Basin Naturalist.* Those larger than 100 printed pages will be considered for the *Memoirs* series.

Illustrations and Tables. All illustrations and tables should be made with a view toward having them appear within the limits of the printed page. The original illustrations or glossy photoprints of them should accompany the manuscript. Illustrations should be prepared for reduction by the printer to either single-column (2⅝ inches) or double-column (5½ inches) width, with the length not exceeding 7½ inches.

Costs Borne by Contributor. Contributors to the *Great Basin Naturalist* should be prepared to donate from $10 to $40 per printed page toward publication of their article (in addition to reprint costs). Excessive or complex tables requiring typesetting may be charged to the author at cost. Authors publishing in the *Great Basin Naturalist Memoirs* may be expected to contribute $40 per printed page in addition to the cost of the printed copies they purchase. No reprints are furnished free of charge.

Reprint Schedule for the *Great Basin Naturalist*

100 copies, minimum cost for 2 pages, $26.
Each additional 2 pages, $6.
Each additional 100 copies, $4 for each 2 pages.
Examples: 300 copies of 10 pages = $82; 200 copies of 13 pages = $86.

Great Basin Naturalist Memoirs

No. 1 The birds of Utah. By C. L. Hayward, C. Cottam, A. M. Woodbury, H. H. Frost. $10.
No. 2 Intermountain biogeography: a symposium. By K. T. Harper, J. L. Reveal et al. $15.
No. 3 The endangered species: a symposium. $6.
No. 4 Soil-plant-animal relationships bearing on revegetation and land reclamation in Nevada deserts. $6.
No. 5 Utah Lake monograph. $8.
No. 6 The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. $60.

TABLE OF CONTENTS

Buccal floor of reptiles, a summary. Wilmer W. Tanner and David F. Avery 273

Western diamondback rattlesnake in southern Nevada: a correction and comments. Frederick H. Emmerson 350

Prevalence of *Elaeophora schneideri* and *Onchocerca cervipedis* in mule deer from central Utah. Lauritz A. Jensen, Jordan C. Pederson, and Ferron L. Andersen 351

Ecomorphology and habitat utilization of *Echinocereus engelmannii* and *E. triglochidiatus* (Cactaceae) in southeastern California. Richard I. Yeaton 353

First specimen of the spotted bat (*Euderma maculatum*) from Colorado. Robert B. Finley, Jr., and James Creasy 360

Status of introduced fishes in certain spring systems in southern Nevada. Walter R. Courtenay, Jr., and James E. Deacon 361

A new species of *Penstemon* (Scrophulariaceae) from the Uinta Basin of Utah and Colorado. John Larry England 367

Phalacropsis dispar (Coleoptera: Phalacridae), an element in the natural control of native pine stem rust fungi in the western United States. David L. Nelson 369

Species-habitat relationships in an Oregon cold desert lizard community. David F. Werschkul 380

Preliminary index of authors of Utah plant names. L. Matthew Chatterley, Blaine T. Welsh, and Stanley L. Welsh 385

Nest site selection in raptor communities of the eastern Great Basin desert. Dwight G. Smith and Joseph R. Murphy 395

Invertebrate faunas and zoogeographic significance of lava tube caves of Arizona and New Mexico. Stewart B. Peck 405

Additions to the vascular flora of Montana and Wyoming. Robert W. Lichvar and Robert D. Dorn 413

3108
✓✓

THE GREAT BASIN NATURALIST

olume 42 No. 4 December 31, 1982 Brigham Young University

MUS. COMP. ZOOL
LIBRARY
[illegible]
HARVARD
UNIVERSITY

GREAT BASIN NATURALIST

Editor. Stephen L. Wood, Department of Zoology, 290 Life Science Museum, Brigham Young University, Provo, Utah 84602.

Editorial Board. Kimball T. Harper, Chairman, Botany; James R. Barnes, Zoology; Hal L. Black, Zoology; Stanley L. Welsh, Botany; Clayton M. White, Zoology. All are at Brigham Young University, Provo, Utah 84602.

Ex Officio Editorial Board Members. Bruce N. Smith, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications.

Subject Area Associate Editors.

Dr. Noel H. Holmgren, New York Botanical Garden, Bronx, New York 10458 (Plant Taxonomy).

Dr. James A. MacMahon, Utah State University, Department of Biology, UMC 53, Logan, Utah 84322 (Vertebrate Zoology).

Dr. G. Wayne Minshall, Department of Biology, Idaho State University, Pocatello, Idaho 83201 (Aquatic Biology).

Dr. Ned K. Johnson, Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720 (Ornithology).

Dr. E. Philip Pister, Associate Fishery Biologist, California Department of Fish and Game, 407 West Line Street, Bishop, California 93514 (Fish Biology).

Dr. Wayne N. Mathis, Chairman, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 (Entomology).

Dr. Theodore W. Weaver III, Department of Botany, Montana State University, Bozeman, Montana 59715 (Plant Ecology).

The *Great Basin Naturalist* was founded in 1939 and has been published from one to four times a year since then by Brigham Young University. Previously unpublished manuscripts in English of less than 100 printed pages in length and pertaining to the biological natural history of western North America are accepted. Western North America is considered to be west of the Mississippi River from Alaska to Panama. The *Great Basin Naturalist Memoirs* was established in 1976 for scholarly works in biological natural history longer than can be accommodated in the parent publication. The *Memoirs* appears irregularly and bears no geographical restriction in subject matter. Manuscripts are subject to the approval of the editor.

Subscriptions. The annual subscription to the *Great Basin Naturalist* for private individuals is $16.00; for institutions, $24.00 (outside the United States, $18.00 and $26.00); and for student subscriptions, $10.00. The price of single issues is $6.00 each. All back issues are in print and are available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to Brigham Young University, *Great Basin Naturalist*, 290 Life Science Museum, Provo, Utah 84602. The *Great Basin Naturalist Memoirs* may be purchased from the same office at the rate indicated on the inside of the back cover of either journal.

Scholarly Exchanges. Libraries or other organizations interested in obtaining either journal through a continuing exchange of scholarly publications should contact the Brigham Young University Exchange Librarian, Harold B. Lee Library, Provo, Utah 84602.

Manuscripts. See *Notice to Contributors* on the inside back cover.

12-82 650 61876

ISSN 017-3614

The Great Basin Naturalist

Published at Provo, Utah, by
Brigham Young University

ISSN 0017-3614

Volume 42 December 31, 1982 No. 4

ANTS OF UTAH

Dorald M. Allred[1]

Abstract.— Distribution records, including 26 maps of specific collection localities and counties are given for 169 species in 29 genera of ants known to occur in Utah. In some cases intraspecific and interspecific morphological variations and behavior are noted. Taxonomic keys are included for the identification of subfamilies, genera, and species.

Like others who have traversed and studied in the deserts of the western United States and seen the cleared areas around the mounds of harvester ants along roadways, or their patterns of occurrence from an aircraft, I have had a desire to learn more about them and their distribution in Utah. Little published information is existent about the ecological distribution of any species of ant in the state. In 1979 I traveled 4000 miles and in 1980 1300 miles along many of the roads of Utah collecting harvester ants (Map 27). My intent to study only the harvesters gave way to basic training as an entomologist to collect specimens wherever and whenever the opportunity arose. Thus, I collected other ants whenever possible. My intent to report only on the harvesters weakened when it became evident from the literature and a study of the specimens in the collections of the universities in Utah that an accumulation of the distributional data for all of the known species of the state would benefit scientists in a variety of disciplines. Together with Rees and Grundmann (1940), who listed 57 species of 18 genera, and Cole (1942), who listed 64 species of 21 genera, this is the third statewide treatment of the ants of Utah. It treats 169 species in 29 genera. This should serve as a basis and stimulus for others to study these interesting arthropods in Utah, where a paucity of information exists concerning many species, particularly their natural history.

Review of Literature

Earliest reports of ants from Utah were made by Cresson (1874). Garrett (1910) listed some honey ants (*Myrmecocystus*) from the state. Grundmann (1939, 1958) studied the ants of Salt Lake County as part of an unpublished master's thesis and published an annotated list of ants of the Glen Canyon Reservoir area as part of archaeological and biological surveys of that region prior to its being filled with water. Rees and Grundmann (1940) published the first *Ants of Utah* based on specimens and data contained in collections of the Department of Biology at the University of Utah. Some of their records are of collections that date back as far as 1902. Cole (1942) published the second *Ants of Utah* based on collections he made, as well as ants sent to him from the University of Utah and Utah State University. Hayward (1945) listed ants taken in a study of the biotic communities of some mountains of Utah. Knowlton (1946, 1963, 1970, 1975) reported on birds feeding on ants, discussed harvester ant control, and published lists of ants collected in Curlew Valley in northern Box Elder County as part of the Desert Biome Studies of the International Biological Program. Knowlton and Nye (1946) reported on lizards feeding on ants. James (1949) made an ecological study of the ants of Red Butte Canyon in eastern Salt Lake County. Bohart and Knowlton (1953) studied the food habits of the western harvester ant. Ingham (1959, 1963) studied the ants of the Virgin River Basin in extreme southwestern Utah, encompassing primarily Washington County, the southern part of Iron County, and the western end of Kane County, and compared the ecological distribution of ants in 18 biotic communities of the Great Basin region in Iron County with the Mohave Desert in Washington County. Beck et al. (1967) published a record of predaceous-scavenger ants of Utah collected during 20 years of trapping rodents as part of a study on the parasitic arthropods of the state. Allred and Cole (1979) published on ants collected in southeastern Utah as part of an ecological study on the environmental impact of electric generating plants in that area. Allred (1980) published notes on the swarming activities of harvester ants as part of his observations contributing to this present paper. Other workers have published incidental records of Utah collections and dealt with species known to occur in the state. Notable among those who have published major works are Olsen (1934), Weber (1947), Creighton (1950), Wilson (1955), M. Smith (1957), Gregg (1963), Wheeler and Wheeler (1963), Buren (1968), Cole (1968), Wing (1968), Francoeur (1973), Snelling (1973, 1976), and D. Smith (1979).

---

[1] Life Science Museum and Department of Zoology, Brigham Young University, Provo, Utah 84602.

METHODS

Utah demonstrates a tremendous variety of ecological habitats, from barren clay hills to sand dunes, from Lower Sonoran desert to montane forests and alpine situations. Within any ecological zone the variety of plant habitats varies extensively, frequently within a short distance.

Most of my collecting was done in desert and low elevation habitats that were acceptable to harvester ants. Little time was spent in cultivated areas, in cities, around domestic dwellings, or in mesic habitats other than some montane forests. In the latter case, relatively little collecting was done in coniferous forests except alongside roads that were connecting links enroute to other harvester ant habitats. Most collections were made adjacent to roads, some of which were major highways, others essentially "cow trails." Specific collecting stops were made approximately every 10 miles when plant communities appeared to be generally uniform over long distances. In areas of frequent vegetative change, or where a distribution borderline was suspected to occur, stops were made every 5 miles. Within these distance guidelines in harvester ant areas, the criterion for a specific site stop was the presence of a harvester mound alongside the road. Otherwise, distance stops were rather strictly held to, and a search was made for any ant colony or single individuals at that particular mileage point. Mileages related to a city were measured from the "entering 'city' " sign at the city limits. Where colonies (nests) could be located, little attention was given to single individuals apart from a nest unless they appeared to be of a different species.

Where possible, a large series of workers (20 or more) was taken, as well as winged males and females and immature stages that were present. Large series are desirable because intraspecific variation in workers of some species is significant, and having all sizes of workers is important for identification. When a sizable series was taken, some were mounted on pins (usually indirectly on paper tips) and others preserved in 70 percent ethyl alcohol. If only a few were taken, then all were stored in alcohol. Manipulation of mandibles, antennae, and legs is necessary for observation of some taxonomic characters in many instances, and dried, pinned specimens are too brittle for such manipulation without significant damage to the specimen.

Mounds or burrows were shallowly excavated only sufficient to collect representative samples, or in the case of the harvesters to determine the presence of winged and immature forms. Relatively few excavations were made under rocks or logs where colonies were exposed by removal of that protective cover.

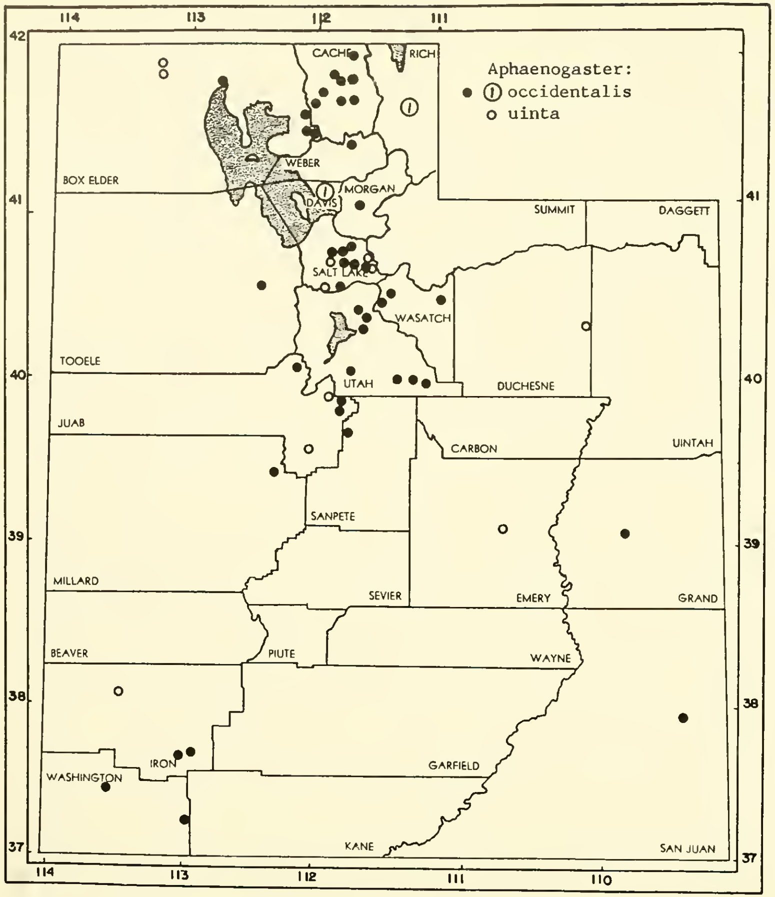
Most ants were retrieved with an aspirator with a large rubber bulb as the vacuum source, an especially useful tool for collecting most of the species. Blowing air from the bulb into the entrance of the nest of some harvesters usually resulted in a "boiling" of the workers from the entrance, and collection of a series required less than a minute. Other species were not so affected, and some, especially in the genus *Formica,* clung tenaciously to the substrate, whereas others attempted to hide under debris or in an exposed tunnel and were picked up with fingers or forceps.

Based on listings and distribution of collection localities, counties that apparently have been most thoroughly collected, likely because of the presence of a major university in the vicinity, are Cache County (except the mountainous southeastern part) by Utah State University, Salt Lake County (except the western and northwestern parts, which are primarily mountainous and salty, mesic areas, respectively) by the University of Utah, and Utah County (except the southwestern part, which is partly mountainous area) by Brigham Young University. Southeastern Iron County, central and eastern Washington County, and western Kane County were fairly well collected by Ingham (1959) in studies for his master's thesis. Plotting of all of the collection localities listed for the state shows an interesting distribution pattern (Map 28). Comparatively speaking, relatively little of the state has been adequately collected, even within many collected (unshaded) areas of the map. The southern and northern areas of Box Elder and Tooele counties, respectively, are covered by salt flats of the Great Salt Lake desert and would be expected to have only rather isolated habitats favorable for ants, such as some of the knolls and mountains above the level of the perennial salt deposits. Other noncollected areas of the state are mountainous, plateau, or desert areas not readily accessible except by four-wheel drive vehicles, horseback, or walking. However, even in some of those areas, limited access is possible because of the building of many roads for mineral explorations in recent years.

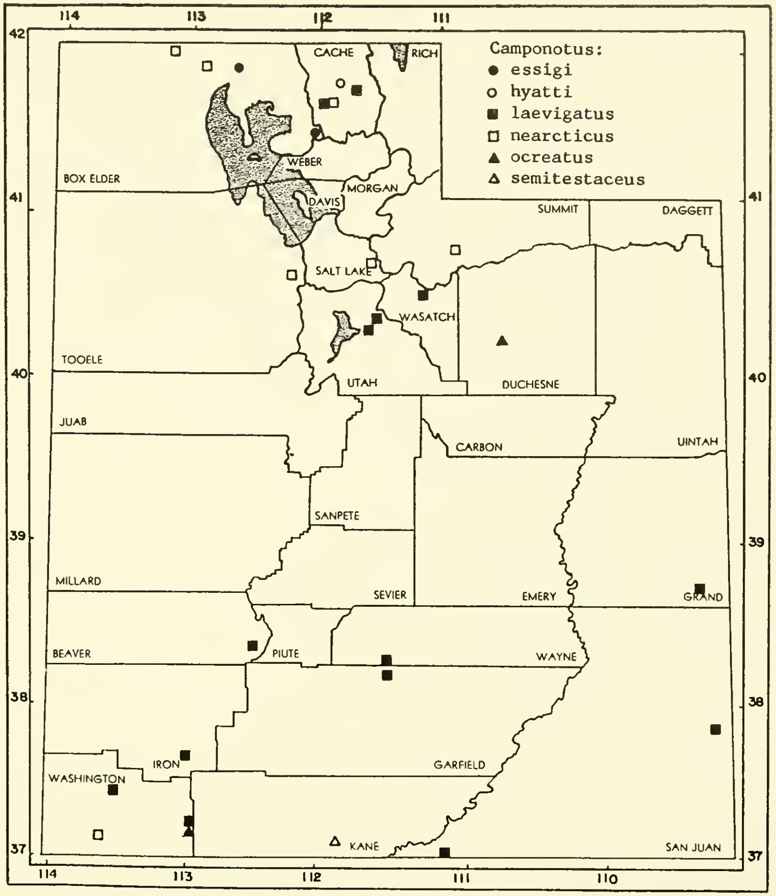
Some areas visited demonstrated a uniqueness of abundance or absence of ants. In the plateau areas of southern Utah where sandstone was the predominant exposed strata, no ants were found under sandstone slabs or boulders, whereas in other parts of the state other types of rocks most frequently sheltered ant colonies. Perhaps one reason for their absence under sandstone was the dryness of the area and inability of the porous sandstone to maintain a moist habitat underneath. In coniferous forest areas where almost pure stands of lodgepole pine occurred, extensive searching in and under fallen logs failed to disclose more than a few ants of any species, particularly the carpenters. In one particular area 13.4 miles north of Utah Highway 121 on the Dry Fork-Red Cloud Loop road in the foothills of the Uinta Mountains in northern Uintah County at an elevation of 7000 ft, a greater diversity of ants was encountered than in any other place in the state. The specific site was a west-facing slope that was covered with many medium-sized to large boulders in a dense stand of sagebrush and snowberry. Ingham (1963) indicated that in southern Utah the greatest numbers of species occur in sagebrush, rabbitbrush, and juniper habitats. About half as many species were found in more alkaline situations supporting greasewood, shadscale, and saltbush. Fewest species were found in Sonoran habitats supporting joshua trees, creosote bush, and bur sage.

Systematics

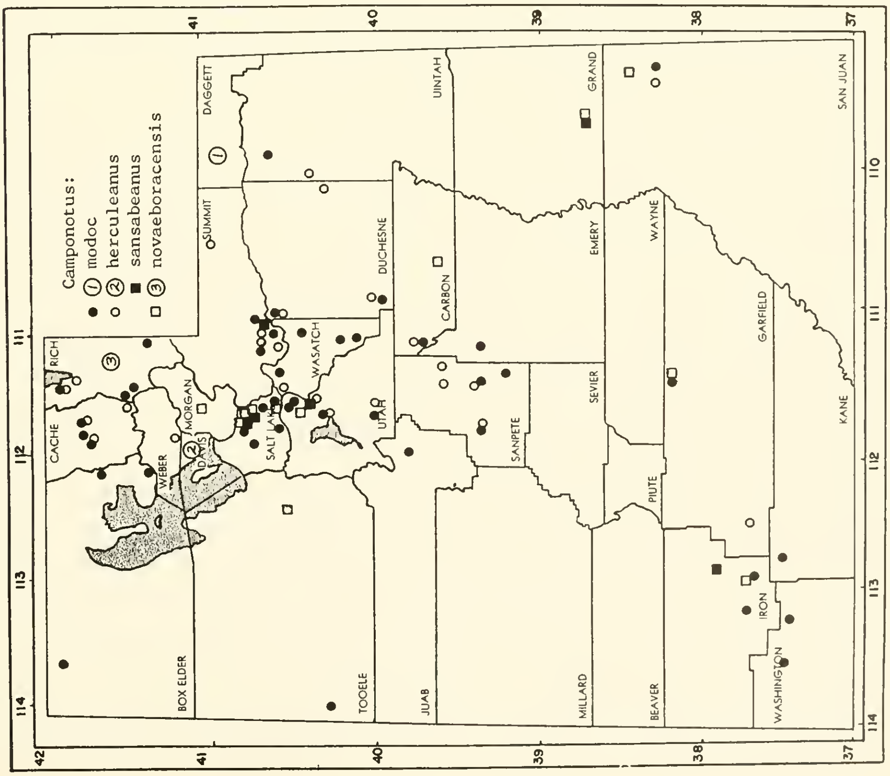
The listing of species in the main body of the report follows Creighton (1950) and Smith (1979) except that I have dropped their subspecies designations. In the keys I have included subspecies and varieties only to their specific level. This is not intended to indicate synonymy, but is only for convenience and brevity. Likewise, species, subspecies, and variety names and references applicable to them (except for the first reference that cites the description of the species) listed immediately under the centered species headings in the body of the report are as recorded in published and


Aphaenogaster:
● ① occidentalis
○ uinta
114
113
112
111
110
42
41
40
39
38
37
CACHE
RICH
BOX ELDER
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
WASATCH
TOOELE
UTAH
DUCHESNE
JUAB
CARBON
UINTAH
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
WASHINGTON
GARFIELD
KANE
SAN JUAN

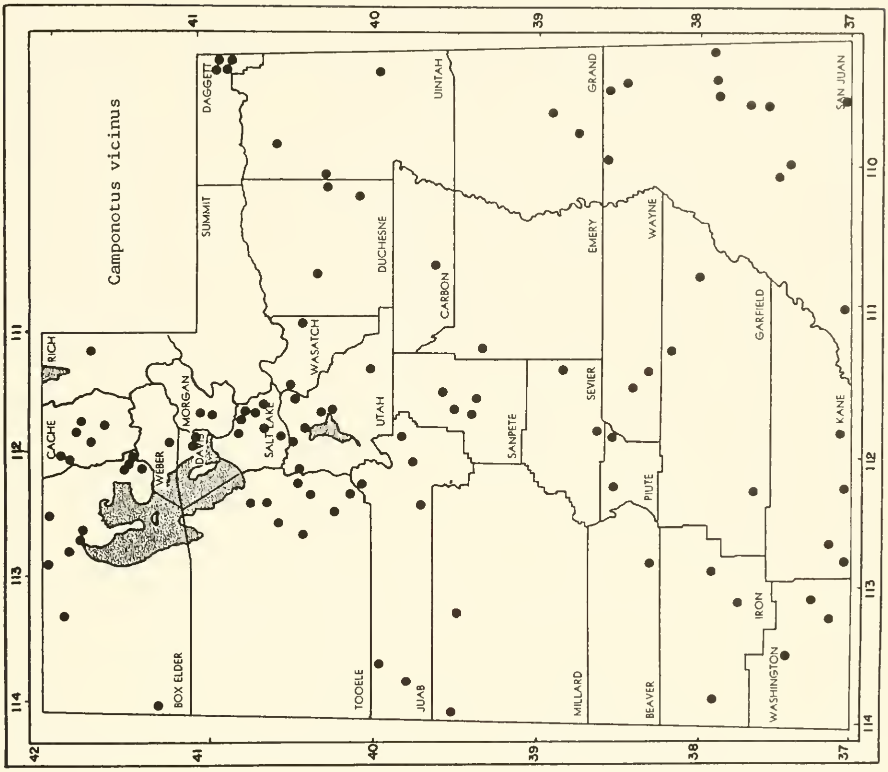
Map 1. Distribution of *Aphaenogaster occidentalis* and *uinta* in Utah. Number in circle indicates specific plot in county unknown.


Camponotus:
● essigi
○ hyatti
■ laevigatus
□ nearcticus
▲ ocreatus
△ semitestaceus
114
113
112
111
110
42
41
40
39
38
37
CACHE
RICH
BOX ELDER
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
WASATCH
TOOELE
UTAH
DUCHESNE
JUAB
CARBON
UINTAH
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
WASHINGTON
GARFIELD
KANE
SAN JUAN

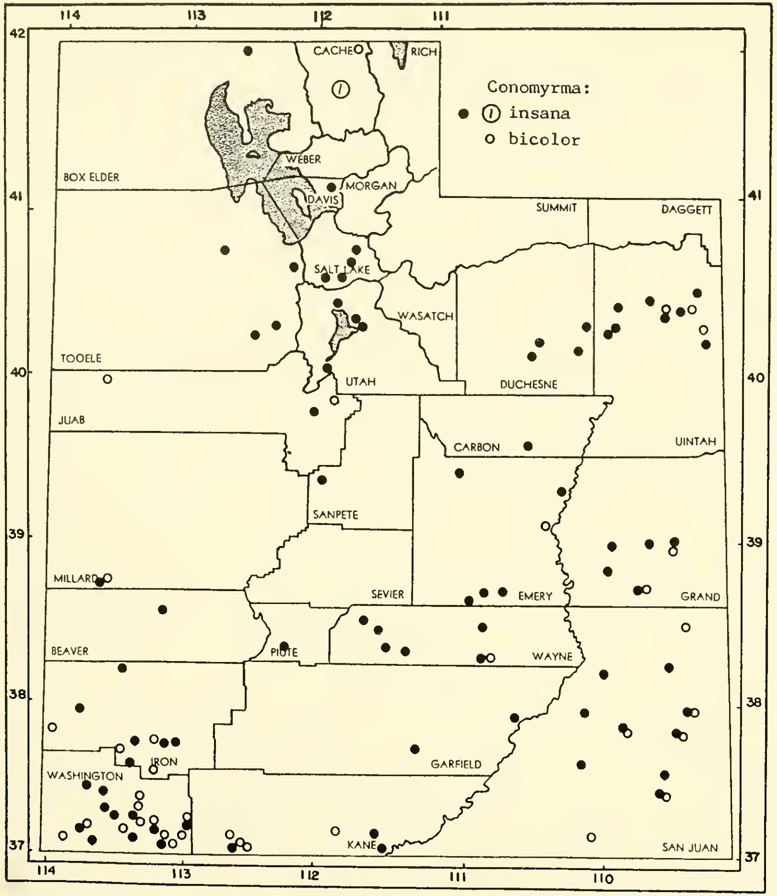
Map 2. Distribution of *Camponotus essigi, hyatti, laevigatus, nearcticus, ocreatus,* and *semitestaceus* in Utah.


Camponotus:
● ① modoc
○ ② herculeanus
■ sansabeanus
□ ③ novaeboracensis
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
UINTAH
DUCHESNE
WASATCH
UTAH
TOOELE
JUAB
CARBON
EMERY
GRAND
SANPETE
SEVIER
MILLARD
WAYNE
PIUTE
BEAVER
GARFIELD
IRON
KANE
SAN JUAN
WASHINGTON
114
113
112
111
110
42
41
40
39
38
37

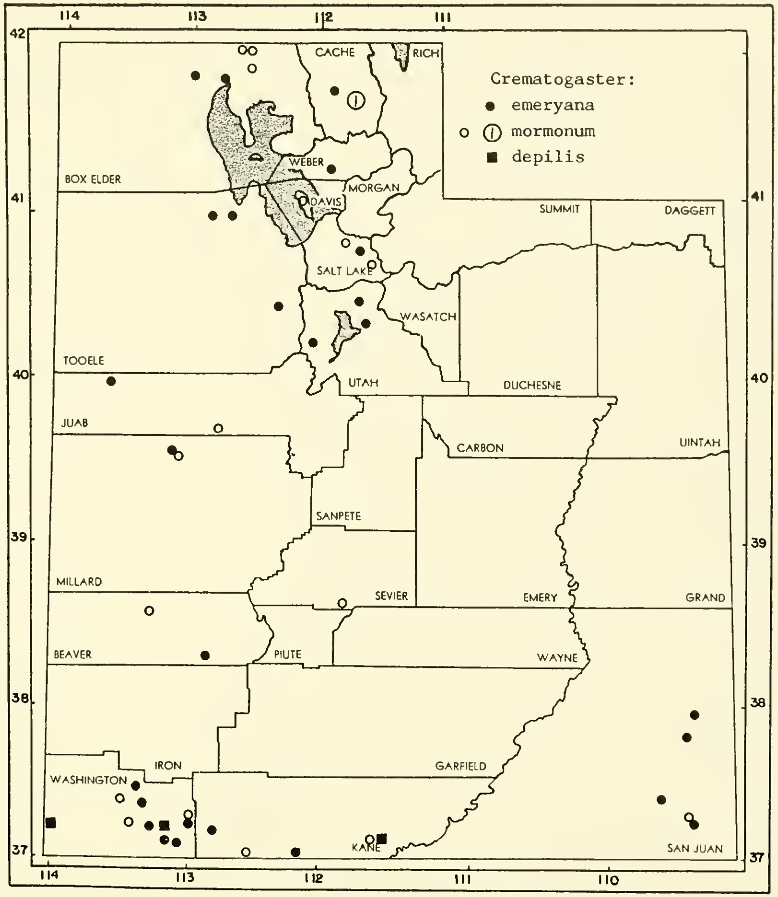
Map 3. Distribution of *Camponotus herculeanus*, *modoc*, *novaeboracensis*, and *sansabeanus* in Utah. Number in circle indicates specific plot in county unknown.


Camponotus vicinus
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
UINTAH
DUCHESNE
WASATCH
UTAH
TOOELE
JUAB
CARBON
EMERY
GRAND
SANPETE
SEVIER
MILLARD
WAYNE
PIUTE
BEAVER
GARFIELD
IRON
KANE
SAN JUAN
WASHINGTON
114
113
112
111
110
42
41
40
39
38
37

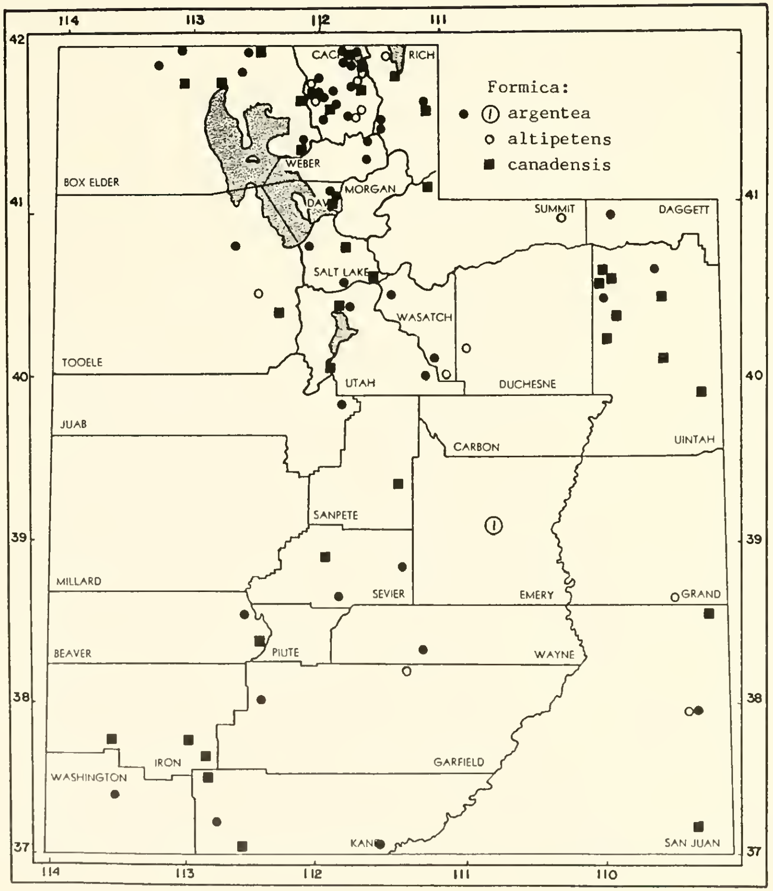
Map 4. Distribution of *Camponotus vicinus* in Utah.


Conomyrma:
● ① insana
○ bicolor
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

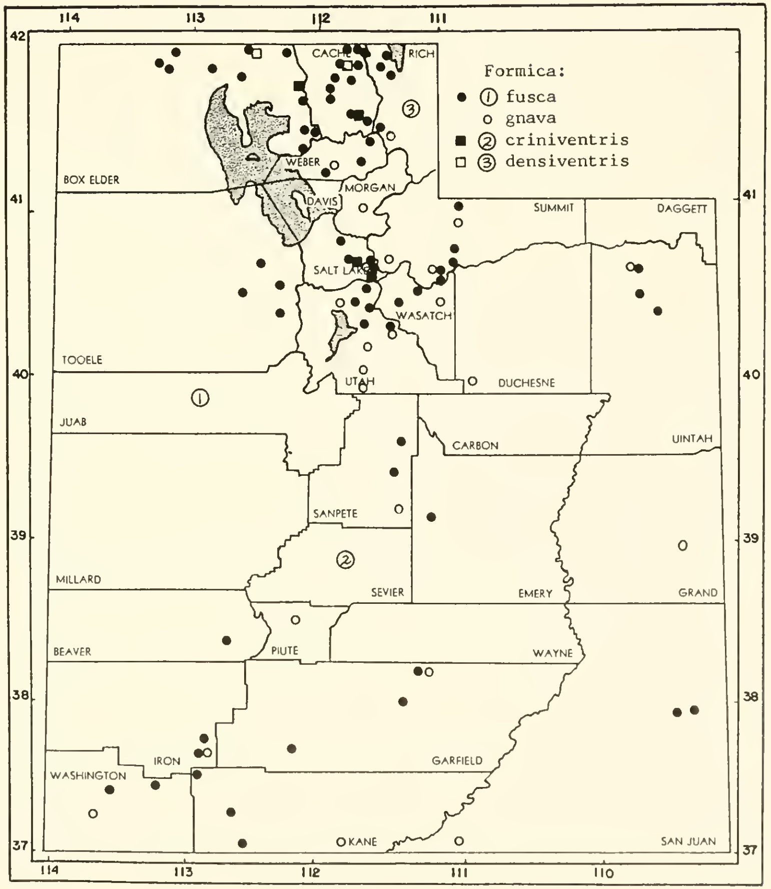
Map 5. Distribution of *Conomyrma bicolor* and *insana* in Utah. Number in circle indicates specific plot in county unknown.


Crematogaster:
● emeryana
○ ① mormonum
■ depilis
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

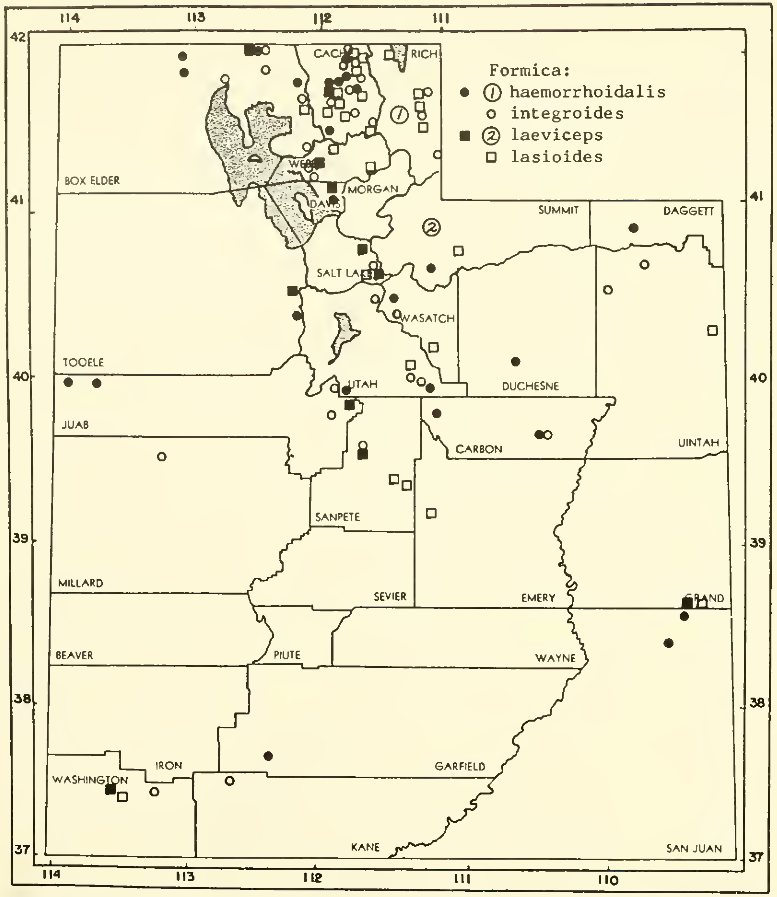
Map 6. Distribution of *Crematogaster depilis, emeryana,* and *mormonum* in Utah. Number in circle indicates specific plot in county unknown.


Formica:
● ① argentea
○ altipetens
■ canadensis
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
WASHINGTON
GARFIELD
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

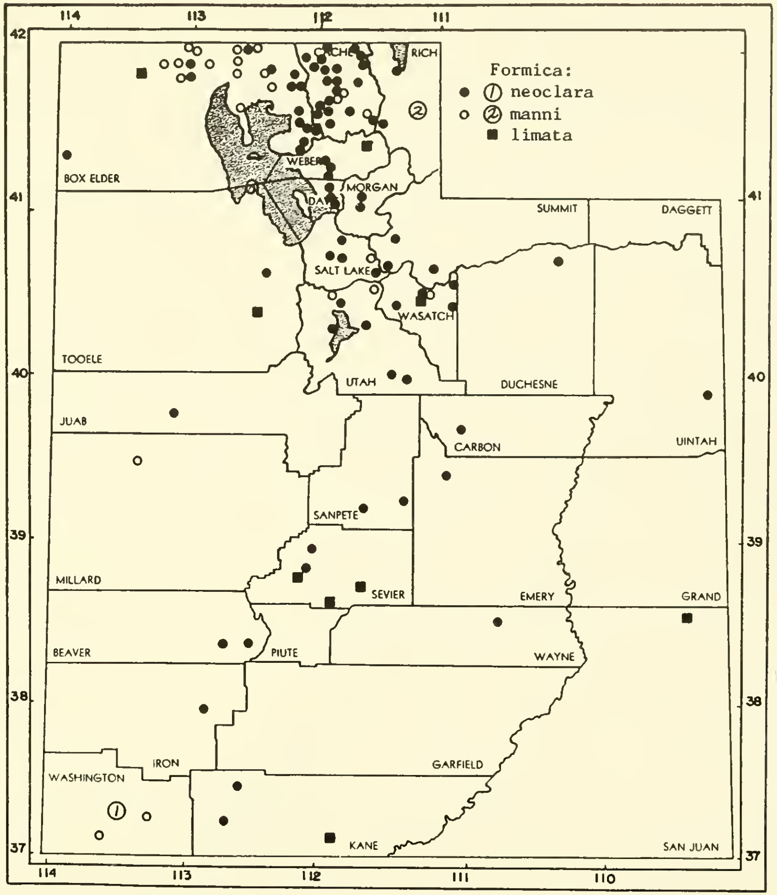
Map 7. Distribution of *Formica altipetens*, *argentea*, and *canadensis* in Utah. Number in circle indicates specific plot in county unknown.


Formica:
● ① fusca
○ gnava
■ ② criniventris
□ ③ densiventris
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
WASHINGTON
GARFIELD
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

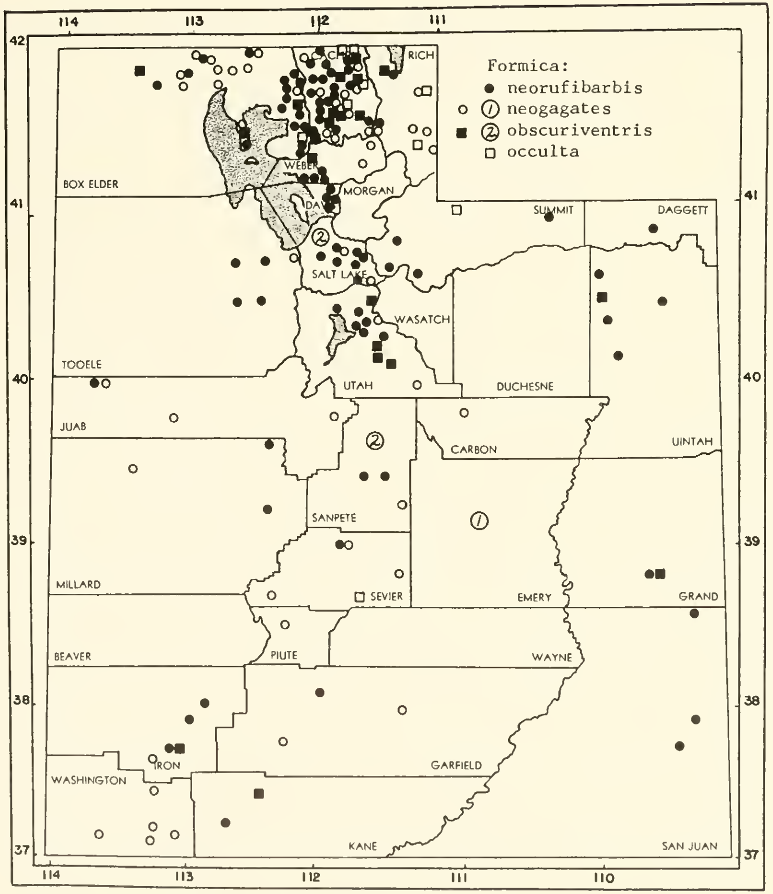
Map 8. Distribution of *Formica criniventris*, *densiventris*, *fusca*, and *gnava* in Utah. Number in circle indicates specific plot in county unknown.


Formica:
● ① haemorrhoidalis
○ integroides
■ ② laeviceps
□ lasioides
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

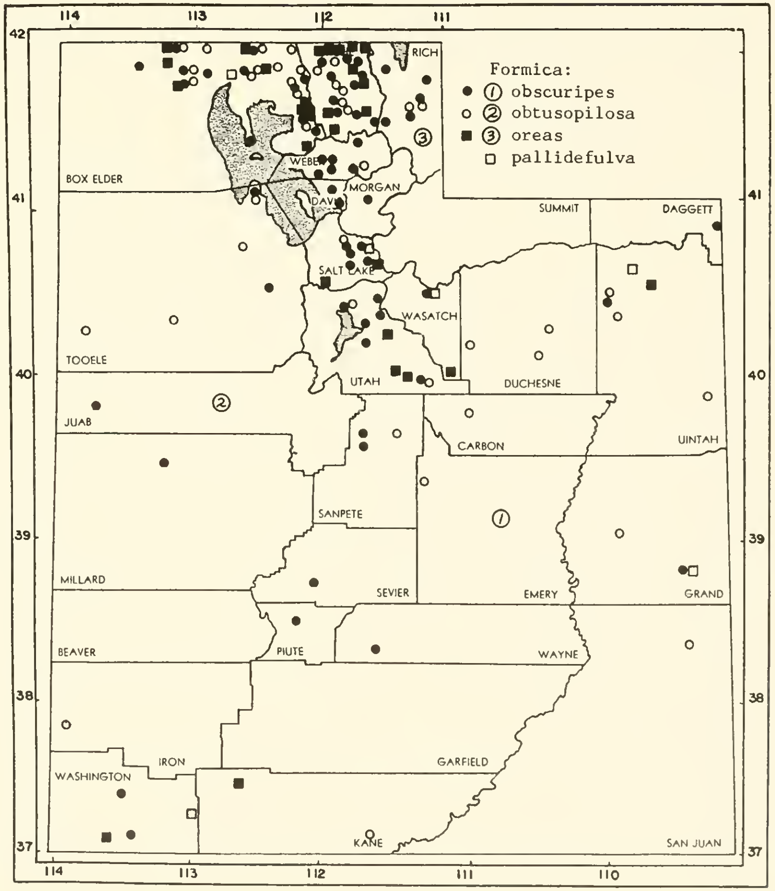
Map 9. Distribution of *Formica haemorrhoidalis, integroides, laeviceps,* and *lasioides* in Utah. Number in circle indicates specific plot in county unknown.


Formica:
● ① neoclara
○ ② manni
■ limata
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

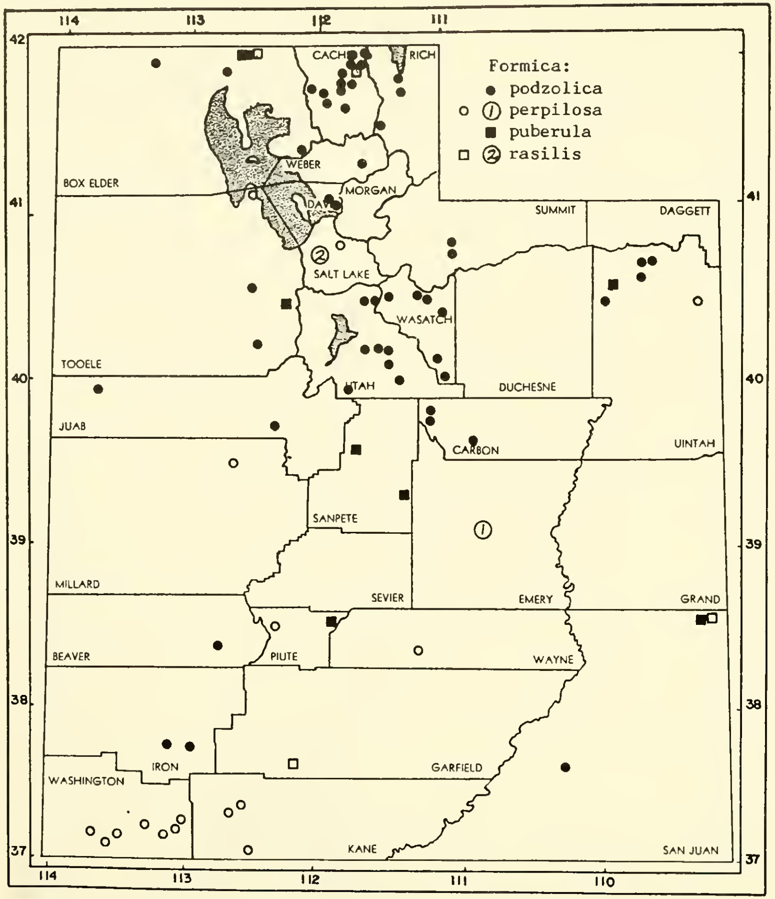
Map 10. Distribution of *Formica limata, manni,* and *neoclara* in Utah. Number in circle indicates specific plot in county unknown.


Formica:
● neorufibarbis
○ ① neogagates
■ ② obscuriventris
□ occulta
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

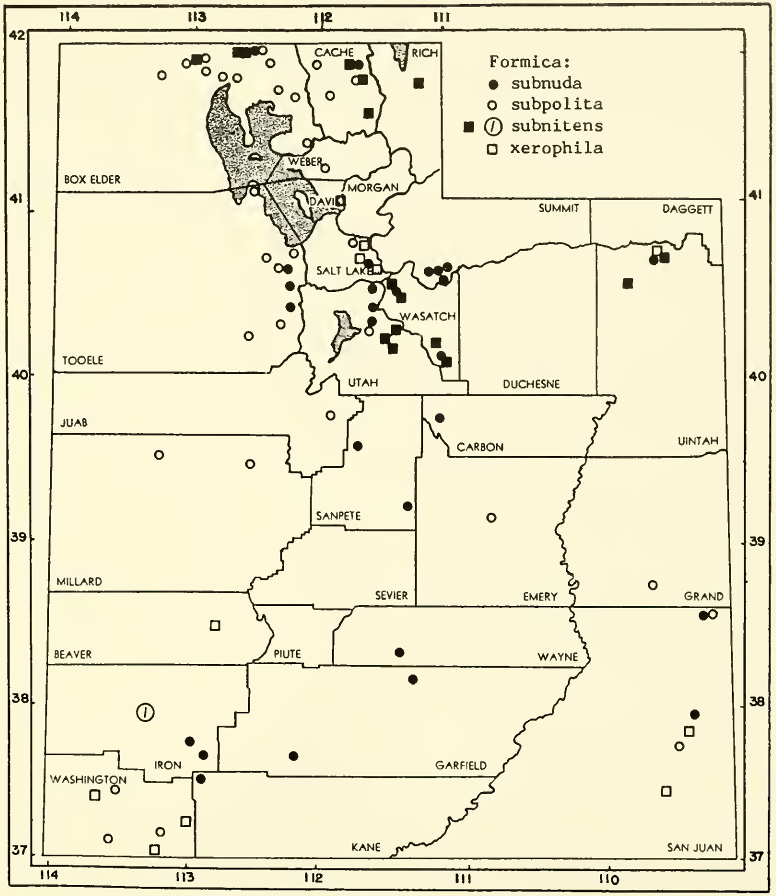
Map 11. Distribution of *Formica neogagates, neorufibarbis, obscuriventris,* and *occulta* in Utah. Number in circle indicates specific plot in county unknown.


Formica:
● ① obscuripes
○ ② obtusopilosa
■ ③ oreas
□ pallidefulva
BOX ELDER
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

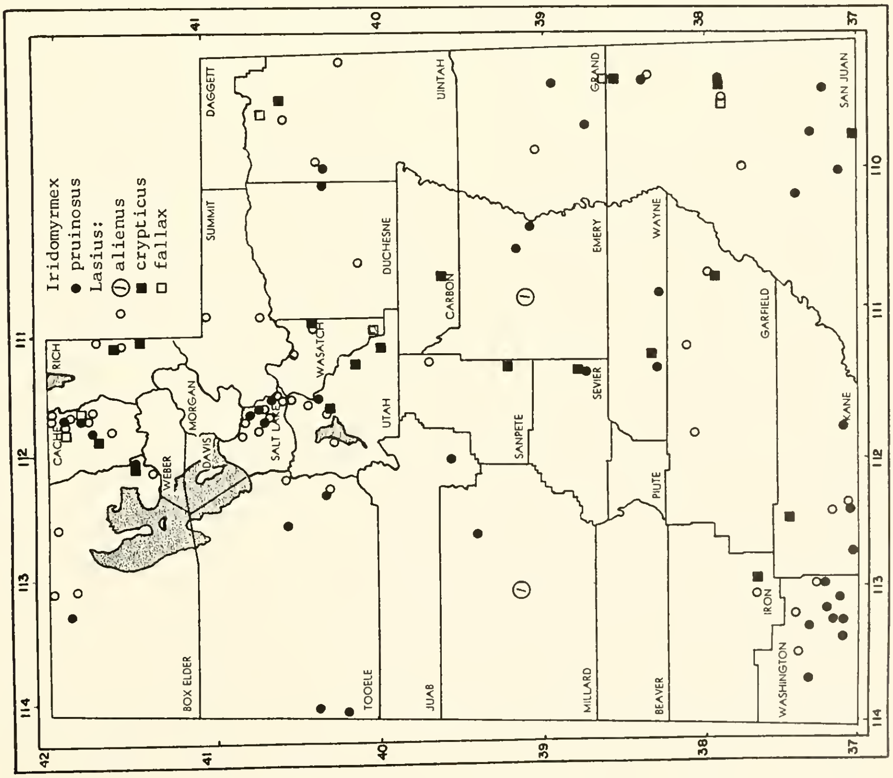
Map 12. Distribution of *Formica obscuripes, obtusopilosa, oreas,* and *pallidefulva* in Utah. Number in circle indicates specific plot in county unknown.


Formica:
● podzolica
○ ① perpilosa
■ puberula
□ ② rasilis
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

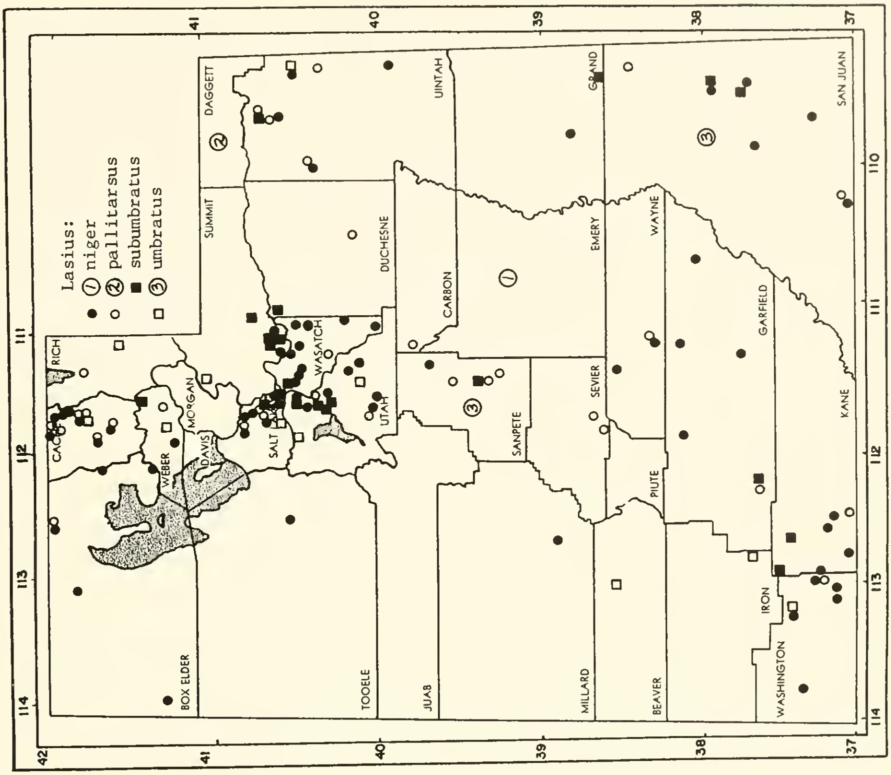
Map 13. Distribution of *Formica perpilosa, podzolica, puberula,* and *rasilis* in Utah. Number in circle indicates specific plot in county unknown.


Formica:
● subnuda
○ subpolita
■ ① subnitens
□ xerophila
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

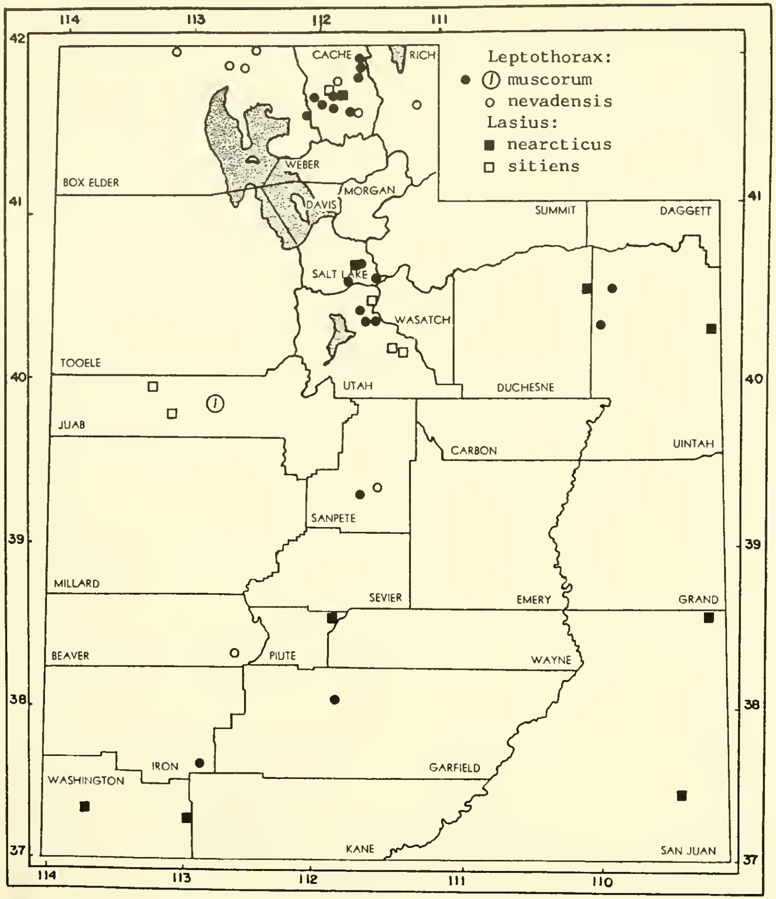
Map 14. Distribution of *Formica subnitens, subnuda, subpolita,* and *xerophila* in Utah. Number in circle indicates specific plot in county unknown.


Iridomyrmex
● pruinosus
Lasius:
○ ① alienus
■ crypticus
□ fallax
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
UINTAH
DUCHESNE
WASATCH
UTAH
TOOELE
JUAB
CARBON
EMERY
GRAND
SANPETE
MILLARD
SEVIER
WAYNE
BEAVER
PIUTE
GARFIELD
SAN JUAN
IRON
KANE
WASHINGTON
42
41
40
39
38
37
114
113
112
111
110

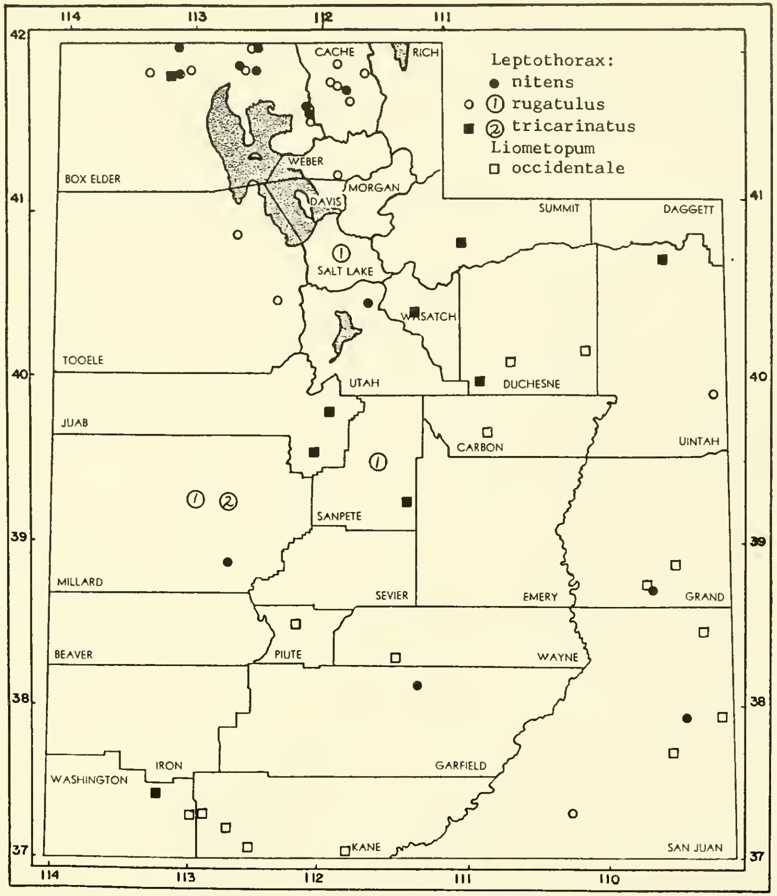
Map 15. Distribution of *Iridomyrmex pruinosus*, *Lasius alienus*, *crypticus*, and *fallax* in Utah. Number in circle indicates specific plot in county unknown.


Lasius:
● ① niger
○ ② pallitarsus
■ subumbratus
□ ③ umbratus
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
UINTAH
DUCHESNE
WASATCH
UTAH
TOOELE
JUAB
CARBON
EMERY
GRAND
SANPETE
MILLARD
SEVIER
WAYNE
BEAVER
PIUTE
GARFIELD
SAN JUAN
IRON
KANE
WASHINGTON
42
41
40
39
38
37
114
113
112
111
110

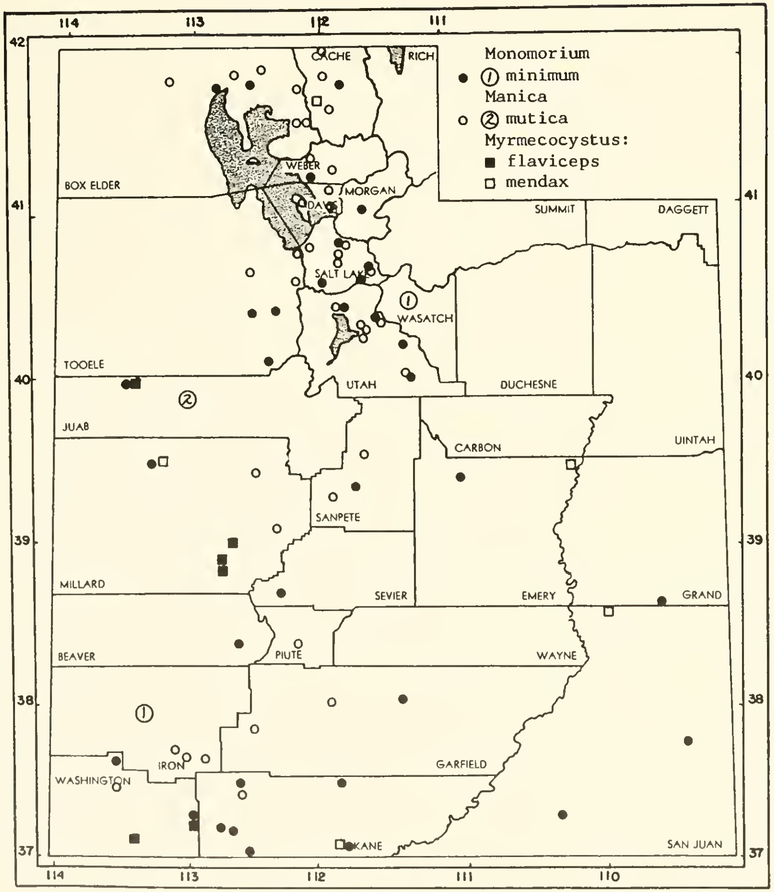
Map 16. Distribution of *Lasius niger*, *pallitarsus*, *subumbratus*, and *umbratus* in Utah. Number in circle indicates specific plot in county unknown.


Leptothorax:
● ① muscorum
o nevadensis
Lasius:
■ nearcticus
□ sitiens
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

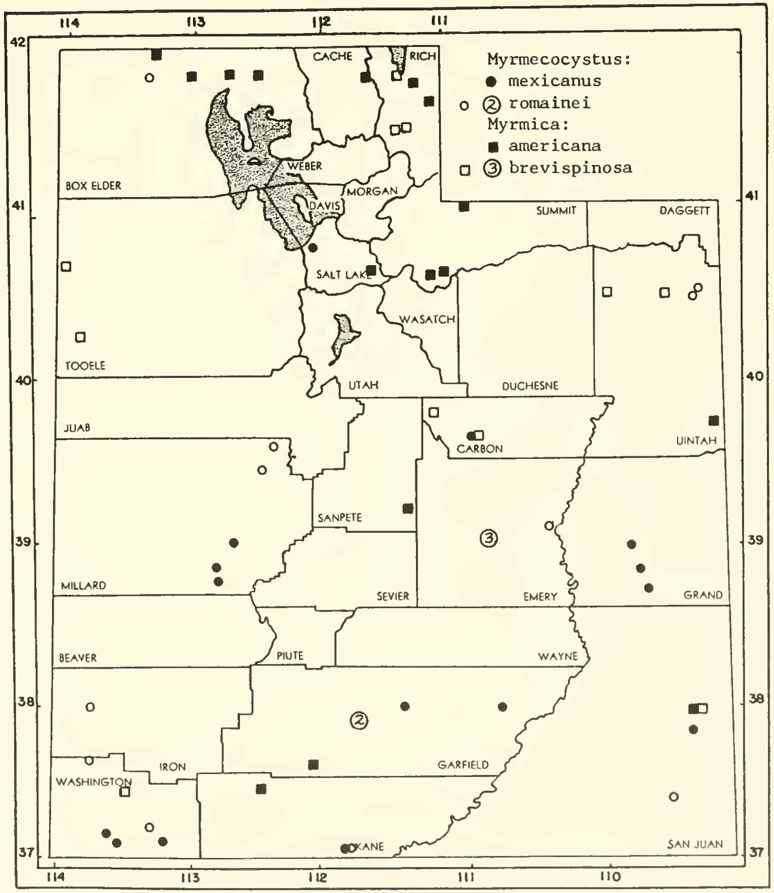
Map 17. Distribution of *Lasius nearcticus, sitiens, Leptothorax muscorum,* and *nevadensis* in Utah. Number in circle indicates specific plot in county unknown.


Leptothorax:
● nitens
o ① rugatulus
■ ② tricarinatus
Liometopum
□ occidentale
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

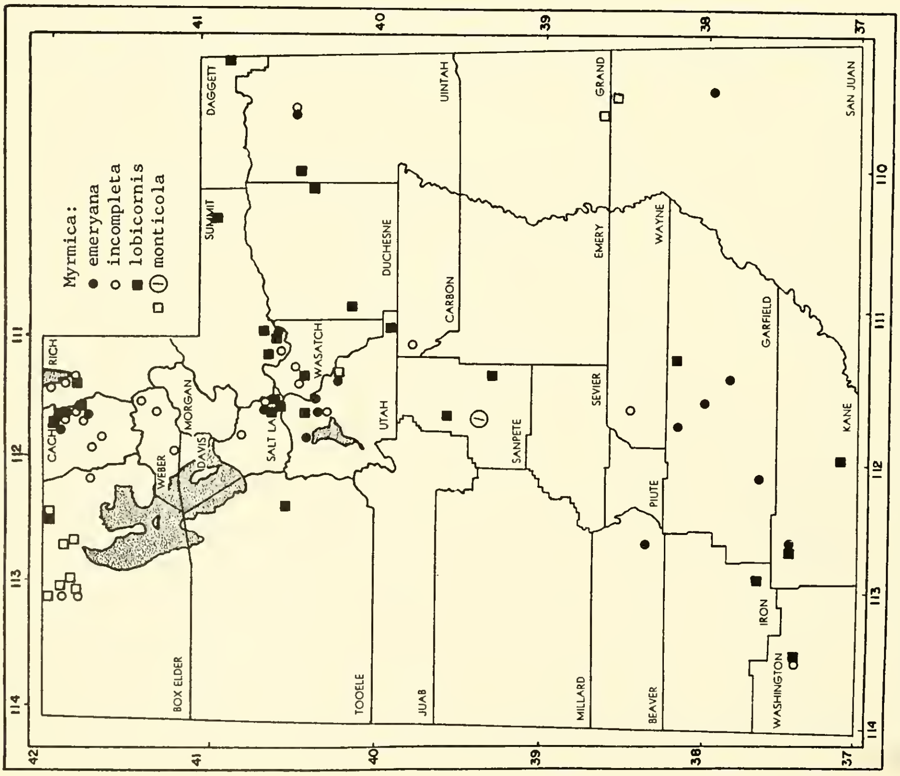
Map 18. Distribution of *Leptothorax nitens, rugatulus, tricarinatus,* and *Liometopum occidentale* in Utah. Number in circle indicates specific plot in county unknown.


Monomorium
● ① minimum
Manica
○ ② mutica
Myrmecocystus:
■ flaviceps
□ mendax
114
113
112
111
110
42
41
40
39
38
37
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
WASATCH
TOOELE
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
①
②

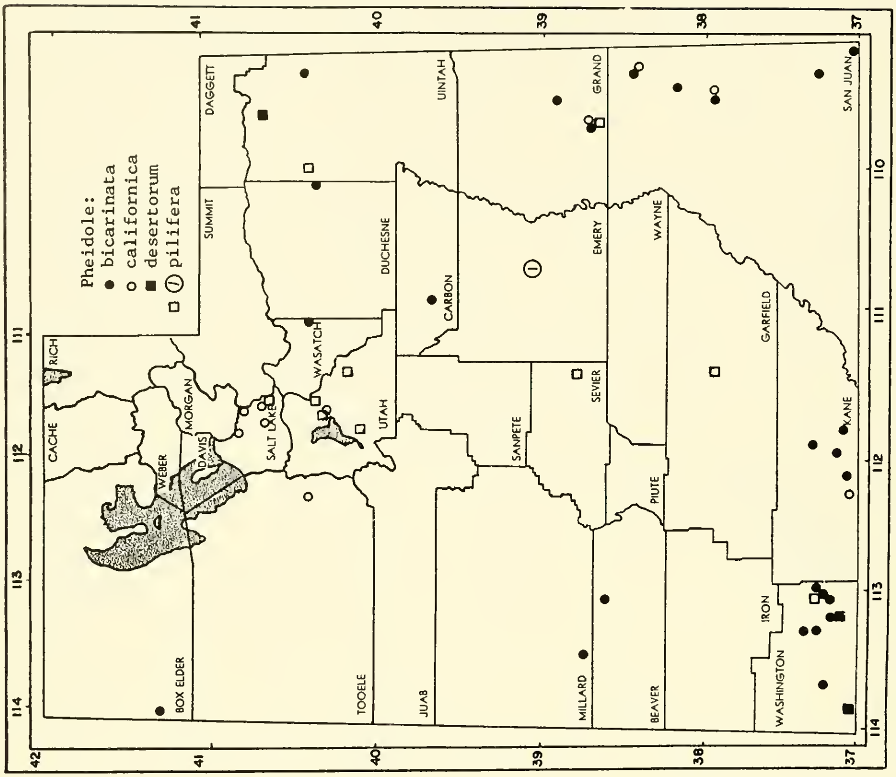
Map 19. Distribution of *Manica mutica*, *Monomorium minimum*, *Myrmecocystus flaviceps*, and *mendax* in Utah. Number in circle indicates specific plot in county unknown.


Myrmecocystus:
● mexicanus
○ ② romainei
Myrmica:
■ americana
□ ③ brevispinosa
114
113
112
111
110
42
41
40
39
38
37
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
WASATCH
TOOELE
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
②
③

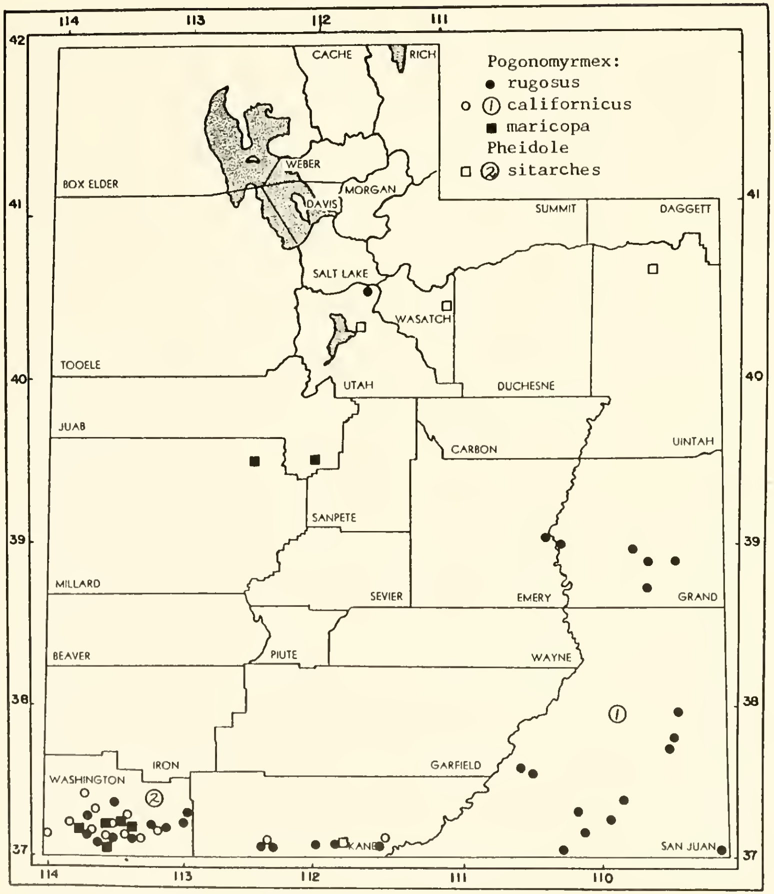
Map 20. Distribution of *Myrmecocystus mexicanus*, *romainei*, *Myrmica americana*, and *brevispinosa* in Utah. Number in circle indicates specific plot in county unknown.


Myrmica:
● emeryana
○ incompleta
■ lobicornis
□ ① monticola
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
WASATCH
DUCHESNE
UINTAH
TOOELE
UTAH
JUAB
CARBON
SANPETE
EMERY
GRAND
MILLARD
SEVIER
BEAVER
PIUTE
WAYNE
GARFIELD
IRON
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

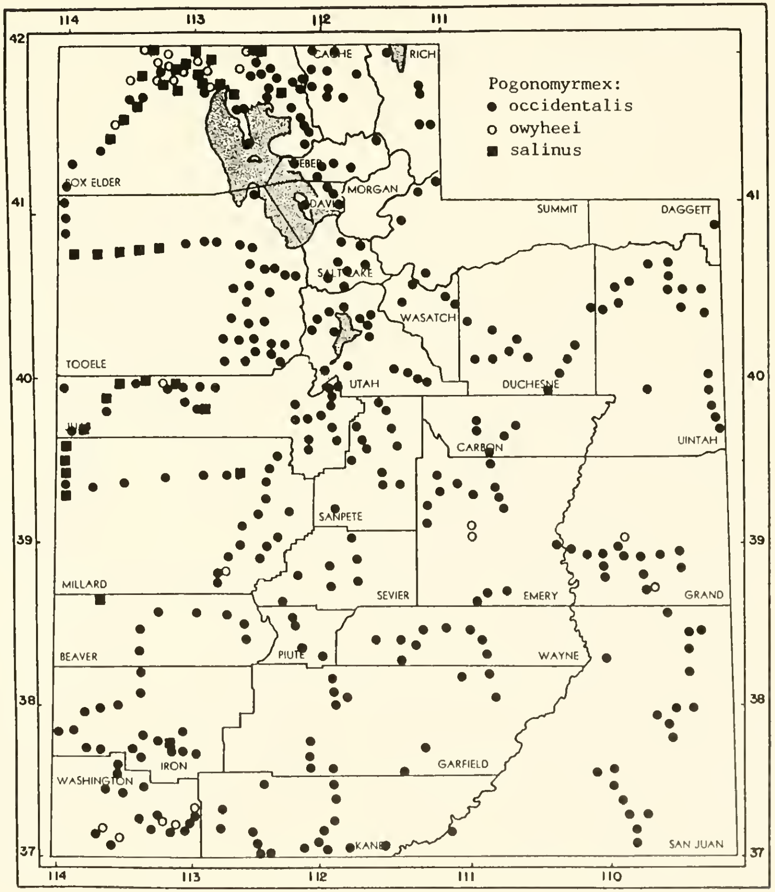
Map 21. Distribution of *Myrmica emeryana, incompleta, lobicornis,* and *monticola* in Utah. Number in circle indicates specific plot in county unknown.


Pheidole:
● bicarinata
○ californica
■ desertorum
□ ① pilifera
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
WASATCH
DUCHESNE
UINTAH
TOOELE
UTAH
JUAB
CARBON
SANPETE
EMERY
GRAND
MILLARD
SEVIER
BEAVER
PIUTE
WAYNE
GARFIELD
IRON
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

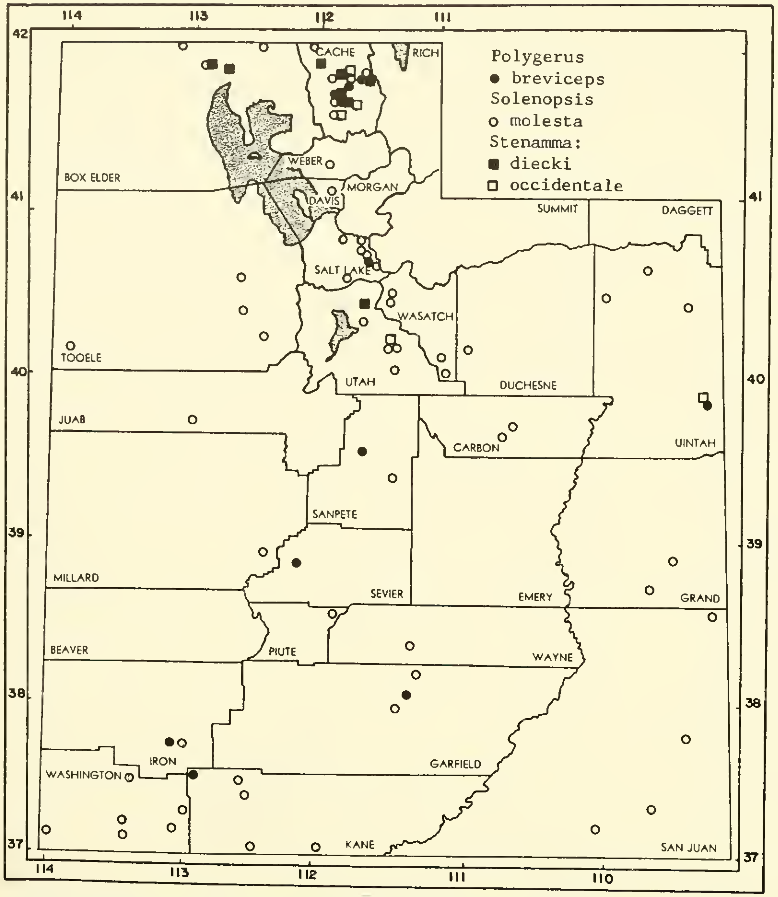
Map 22. Distribution of *Pheidole bicarinata, californica, desertorum,* and *pilifera* in Utah. Number in circle indicates specific plot in county unknown.


Pogonomyrmex:
● rugosus
○ ① californicus
■ maricopa
Pheidole
□ ② sitarches
114
113
112
111
110
42
41
40
39
38
37
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
WASATCH
TOOELE
UTAH
DUCHESNE
JUAB
CARBON
UINTAH
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
WASHINGTON
GARFIELD
KANE
SAN JUAN

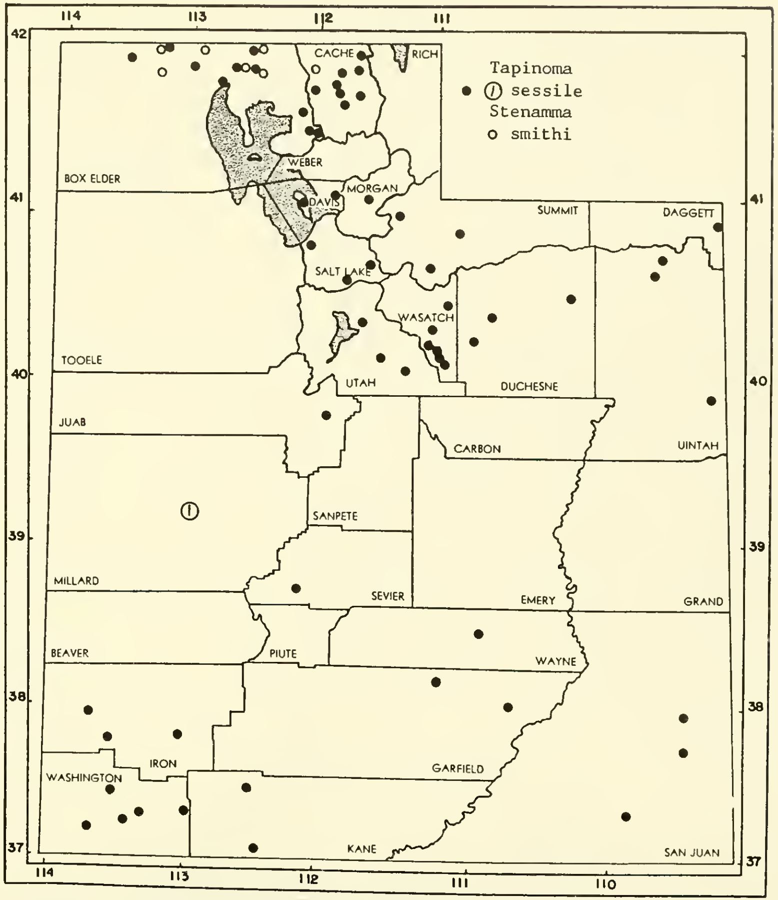
Map 23. Distribution of *Pheidole sitarches*, *Pogonomyrmex californicus*, *maricopa*, and *rugosus* in Utah. Number in circle indicates specific plot in county unknown.


Pogonomyrmex:
● occidentalis
○ owyheei
■ salinus
114
113
112
111
110
42
41
40
39
38
37
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
WASATCH
TOOELE
UTAH
DUCHESNE
JUAB
CARBON
UINTAH
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
WASHINGTON
GARFIELD
KANE
SAN JUAN

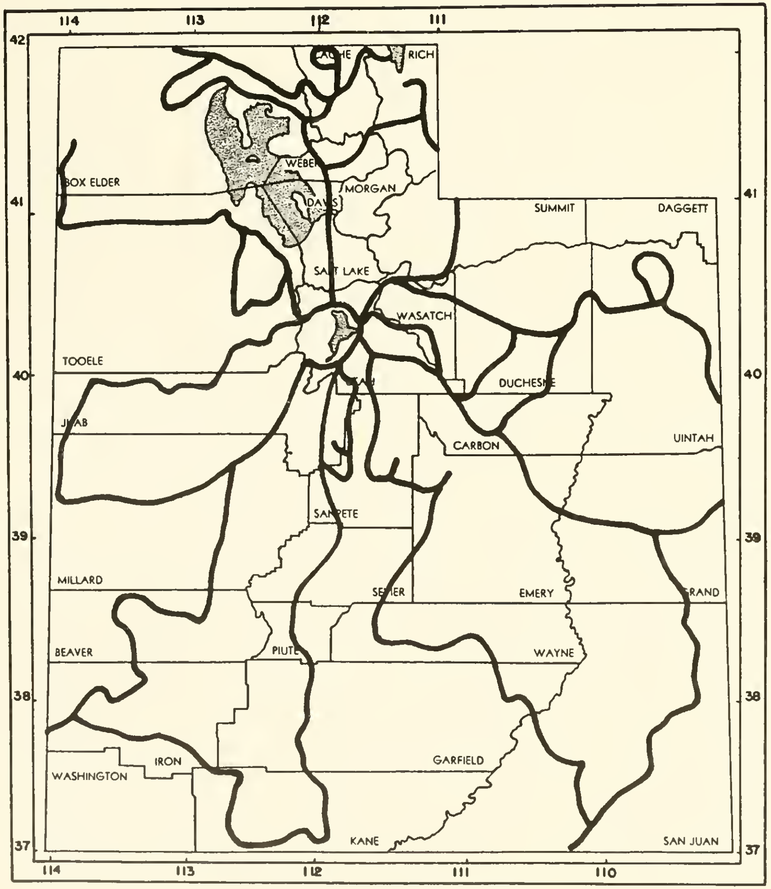
Map 24. Distribution of *Pogonomyrmex occidentalis*, *owyheei*, and *salinus* in Utah.


Polygerus
● breviceps
Solenopsis
○ molesta
Stenamma:
■ diecki
□ occidentale
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

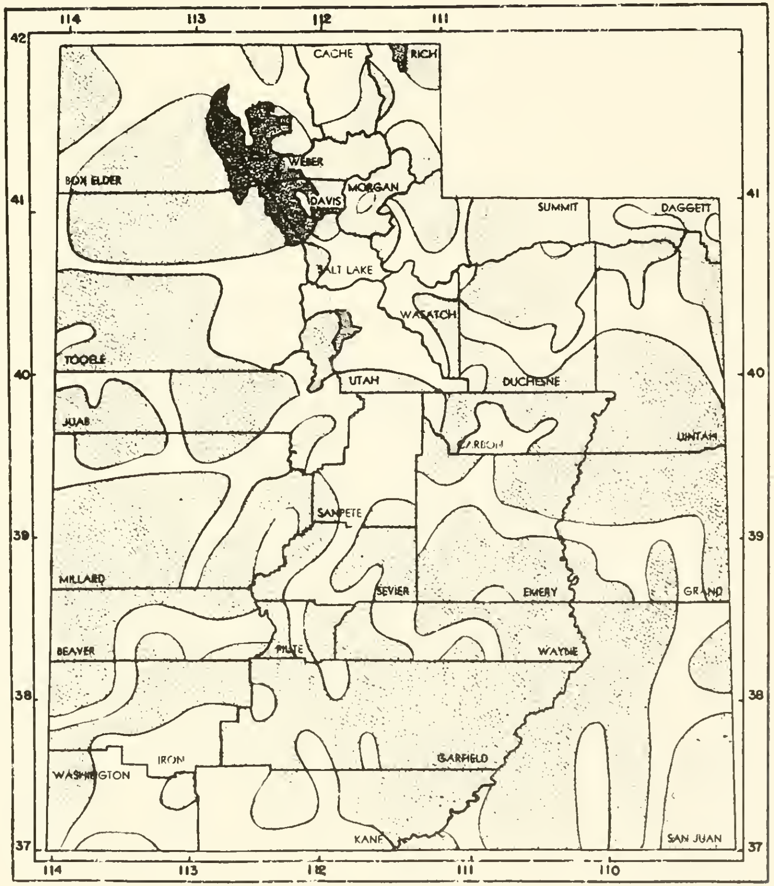
Map 25. Distribution of *Polygerus breviceps*, *Solenopsis molesta*, *Stenamma diecki*, and *occidentale* in Utah.


Tapinoma
● ① sessile
Stenamma
○ smithi
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SUMMIT
DAGGETT
SALT LAKE
TOOELE
WASATCH
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
WASHINGTON
KANE
SAN JUAN
114
113
112
111
110
42
41
40
39
38
37

Map 26. Distribution of *Stenamma smithi*, and *Tapinoma sessile* in Utah. Number in circle indicates specific plot in county unknown.


114
113
112
111
110
42
41
40
39
38
37
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
WASATCH
TOOELE
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
WASHINGTON
GARFIELD
KANE
SAN JUAN

Map 27. Collecting routes of the author in 1979 and 1980.


114
113
112
111
110
42
41
40
39
38
37
BOX ELDER
CACHE
RICH
WEBER
MORGAN
DAVIS
SALT LAKE
SUMMIT
DAGGETT
WASATCH
TOOELE
UTAH
DUCHESNE
UINTAH
JUAB
CARBON
SANPETE
MILLARD
SEVIER
EMERY
GRAND
BEAVER
PIUTE
WAYNE
IRON
WASHINGTON
GARFIELD
KANE
SAN JUAN

Map 28. Areas of ant collections in Utah (clear areas). Shaded areas indicate where no (or few) collections have been reported.

unpublished data for Utah records, and are not intended as synonyms except in those cases as indicated by Creighton (1950), Smith (1979), and other contemporary workers. These and other names applicable to unpublished records and identification labels on specimens in collections examined are given in a separate list at the end of this paper as a means to relate those names to the ones I have used in the body of this report. Where two or more subspecies under a given species have been reported from Utah, they can be separated by characters discussed under the respective species listing in the main body of the paper.

In the treatment of species, generic and trivial names are listed alphabetically in the form of a checklist without regard to subfamily designations, which may be ascertained by reference to the keys. This facilitates location of a species where an index is not present, and extensive searching need not be done by the person who is not well versed in its phylogenetic placement.

Terminology in the keys to subfamilies, genera, and species has been simplified to the lay person's language as far as possible to avoid frustration for those who are not well versed in taxonomic jargon. A glossary of most of the structures referred to in the keys is included, and many structures are figured. Figures 1 and 9 will help in overall structural orientation (Figure 8 was deleted).

Glossary

Abdomen: the hindmost of the three major body regions of an insect, situated behind the thorax.

Antennal club: last two or three antennal segments that are abruptly enlarged to form clublike appearance, sometimes gradually enlarged to much larger terminal segment.

Antennal fossa: pit or base of antenna where it attaches to head.

Clavate: clubbed, gradually thickening toward tip.

Clypeus: the broad plate, frequently triangular, situated on the front of the head between the base of the antennae and the mandibles.

Depressed: flattened or indented.

Epinotum (propodeum of some authors): the posterior major subdivision of the thorax (the second major body part of the ant), actually a structural part of the abdomen anterior to the pedicel, fused to the thorax.

Erect hair: a hair projecting at essentially a right angle to the surface of the integument.

Eye length: maximum measureable length, usually from ventral to dorsal (anterior to posterior).

Facet: one of the small lenses of the compound (large) eye.

Femur: the third segment of the leg (first long one from the base).

Flexor surface: that surface of the segment of a leg that faces and comes close to another such surface when a leg is bent.

Fossa: a pit or deep groove.

Frontal area: a small triangular plate attached to the dorsal edge of the clypeus, situated between the bases of the antennae.

Frontal carina: a distinct ridge or line running upward from the clypeus, and separating the cheek and antennal base from the median part of the head.

Funiculus: that part of the antenna terminal to the scape (the first greatly elongated segment attached to the head) consisting of 8 to 11 segments.

Gaster: the globular or ovoid segments of the abdomen posterior to the pedicel.

Gena: area of head below and behind posterior margin of eye.

Head length: maximum measureable length from ventral (anterior) border of clypeus to median dorsal (posterior) border of head, or to line equal with corners if posterior edge of head is concave.

Head width: maximum width of head exclusive of compound eyes if they extend beyond lateral margins of head.

Humeral angle: the shoulder angle of the prothorax.

Impressed: shallow depressed area or marking.

Integument: the outer covering of the body.

Keel: a sharply angled, elevated ridge.

Labial palps: the two antennalike appendages from the lower lip situated between the mandibles.

Major: a worker of the largest subcaste.

Mandible: one of the paired, heavily chitinized and usually toothed processes on the extreme lateroventral sides of the head.

Maxillary palps: the antennalike appendages from the second jaws situated on each side between the mandibles and the labium (lower lip).

Mesepinotal suture: the transverse indentation that separates the mesonotum from the epinotum.

Mesonotum: dorsal surface of mesothorax.

Mesopleura: side of mesothorax.

Mesothorax: the second major subdivision of the thorax (the second major part of the ant).

Metasternum: the ventral area of the thorax between coxae 3.

Minor: a worker of the smallest subcaste.

Pedicel: the one or two segments between the thorax and gaster, much reduced in diameter and sometimes bearing a scale.

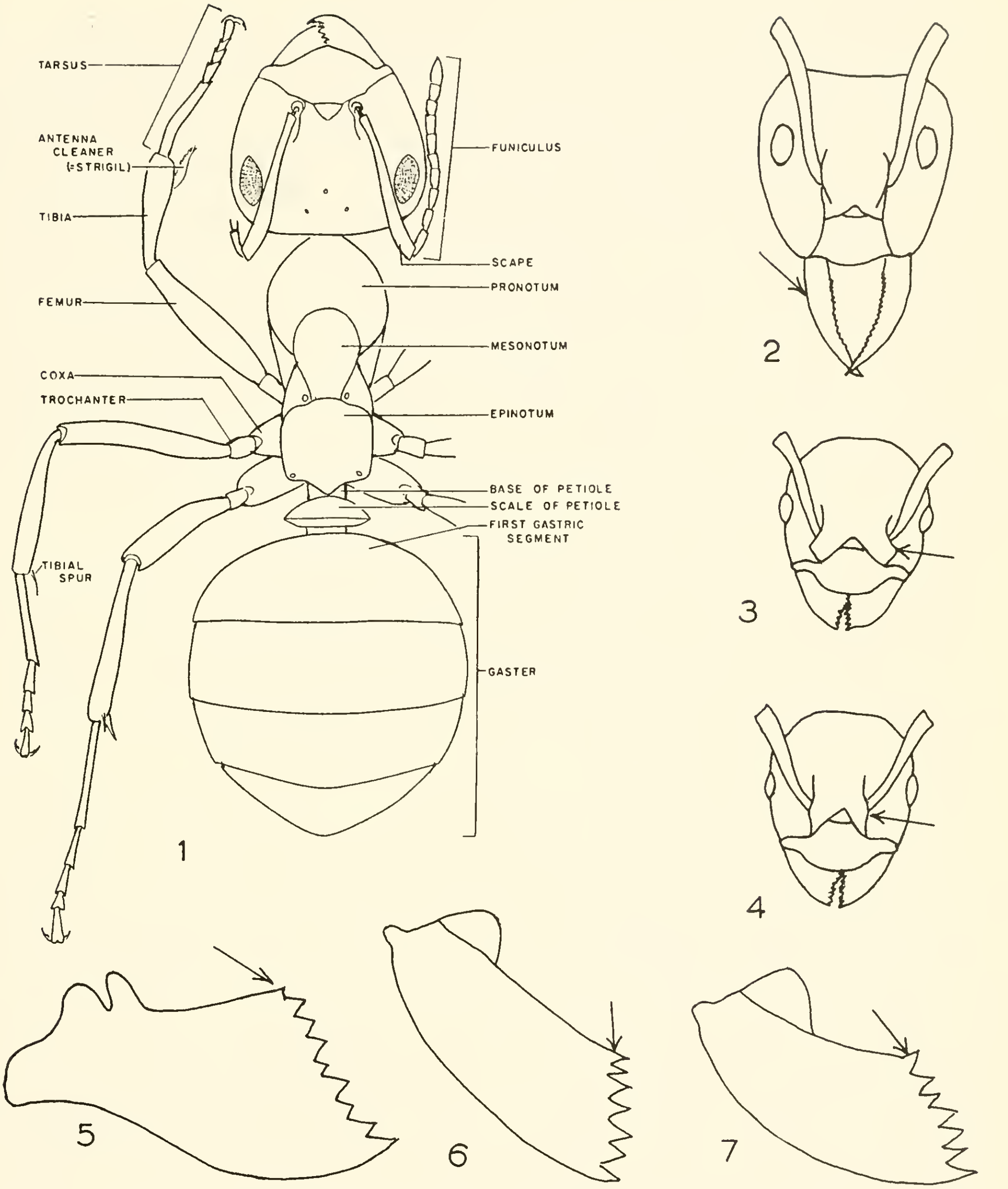
Petiole: a single-segmented pedicel, or the first segment of a two-segmented pedicel.

Postpetiole: the posterior segment of a two-segmented pedicel.

Pronotum: the dorsal surface of the prothorax.

Prothorax: the anterior major subdivision of the thorax (the second major part of the ant).

Psammophore: two rows of long hairs or bristles, one row on each side of the underside of the head.


TARSUS
ANTENNA CLEANER (=STRIGIL)
TIBIA
FEMUR
COXA
TROCHANTER
TIBIAL SPUR
FUNICULUS
SCAPE
PRONOTUM
MESONOTUM
EPINOTUM
BASE OF PETIOLE
SCALE OF PETIOLE
FIRST GASTRIC SEGMENT
GASTER
1
2
3
4
5
6
7

Figs. 1–7. 1, Dorsal view of worker showing major structures (from Wheeler and Wheeler 1963); 2, Sickle-shaped mandibles; 3, Frontal carinae covering antennal insertions, and strongly projected laterally; 4, Frontal carinae not strongly projecting laterally; 5, Triangular mandible with large teeth, the basal tooth offset from other teeth; 6, Basal tooth aligned with other teeth and with mandibular margin; 7, Basal tooth offset and at angle to mandibular margin.

Pubescence: a covering of fine soft hairs, usually lying flat against the integument.

Puncta: minute holes or pits in the integument.

Punctate: possessing puncta.

Ruga: see Wrinkle.

Scale of petiole: a scalelike, somewhat oval vertical or angled projection arising from the dorsal surface of the petiole.

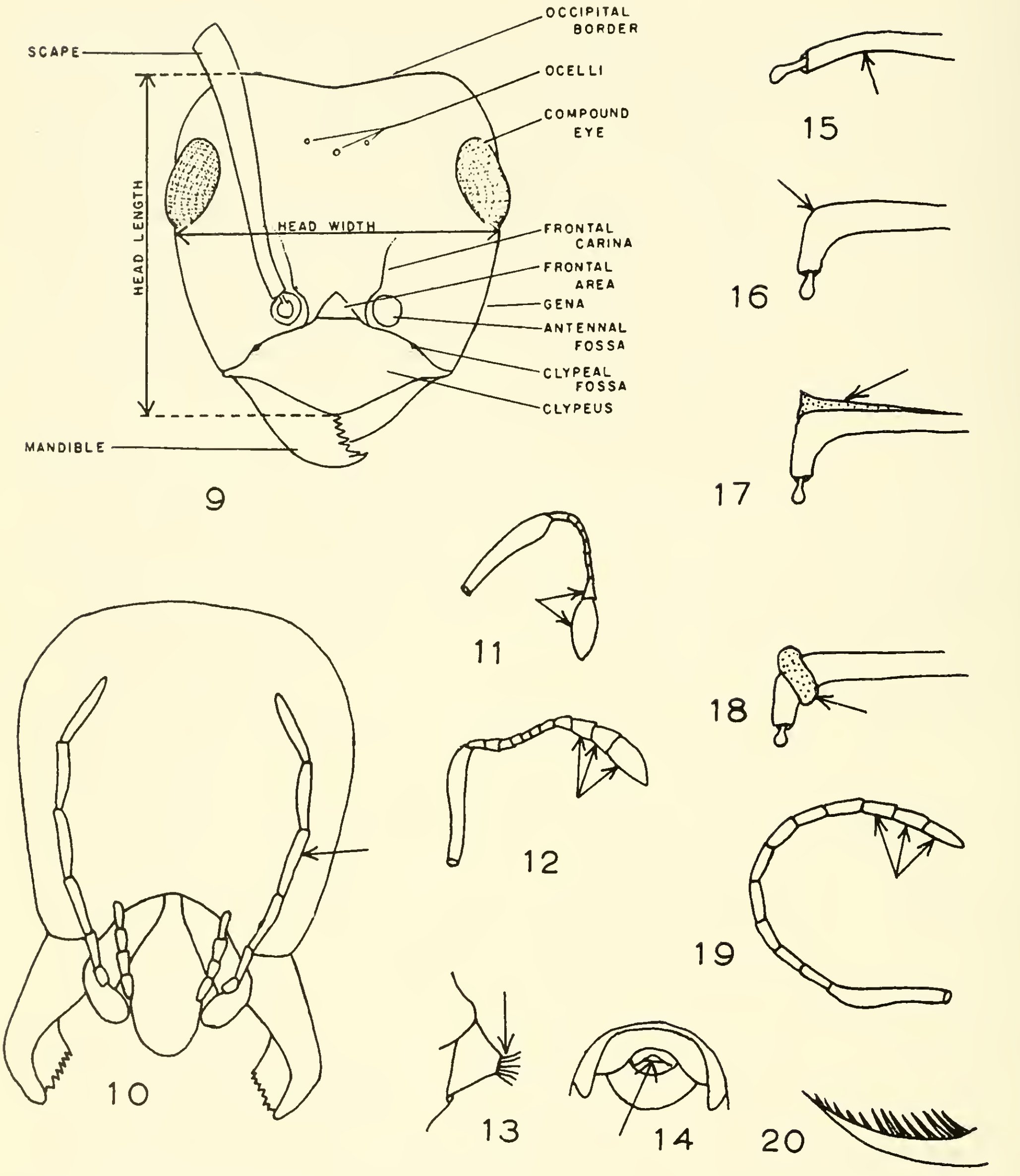
Scale of scape: thick plate at base of scape.

Scape: first greatly elongated segment of the antenna attached to the head.

Sculptured: pattern of elevations and depressions on the integument.

Spinasternal cavity: a minute cavity situated on the ventral side of the metathorax medially between coxae 2 and 3 (can be seen only by removing coxae 2 and 3 on one side).

Striae: longitudinal impressed lines.


OCCIPITAL BORDER
SCAPE
OCELLI
COMPOUND EYE
HEAD LENGTH
HEAD WIDTH
FRONTAL CARINA
FRONTAL AREA
GENA
ANTENNAL FOSSA
CLYPEAL FOSSA
CLYPEUS
MANDIBLE
9
15
16
17
11
10
18
12
19
13
14
20

Figs. 9–20. 9, Frontal view of head of worker showing structures and areas of measurement (from Wheeler and Wheeler 1963); 10, Ventral view of head showing short 4-segmented labial palps and longer 6-segmented maxillary palps; 11, 10-segmented antenna with 2-segmented club; 12, 12-segmented antenna with club of 3 or more segments; 13, Terminal, circular anus fringed with hairs; 14, Subterminal, slitlike anus not fringed with hairs; 15, Scape evenly curved near base; 16, Scape abruptly bent at base; 17, Scape with lobed plate extending one-third along its length; 18, Scape with basal collar or flange; 19, 12-segmented antenna without club; 20, Toothed tibial spur of coxa 3.

Suberect hair: a small hair that projects from the integument at an angle less than 90 degrees but more than 45 degrees.

Tergite: the dorsal plate or surface of a segment, usually applicable to the gaster.

Thorax: second major division of ant between head and pedicel, composed of prothorax, mesothorax, and epinotum ("metathorax").

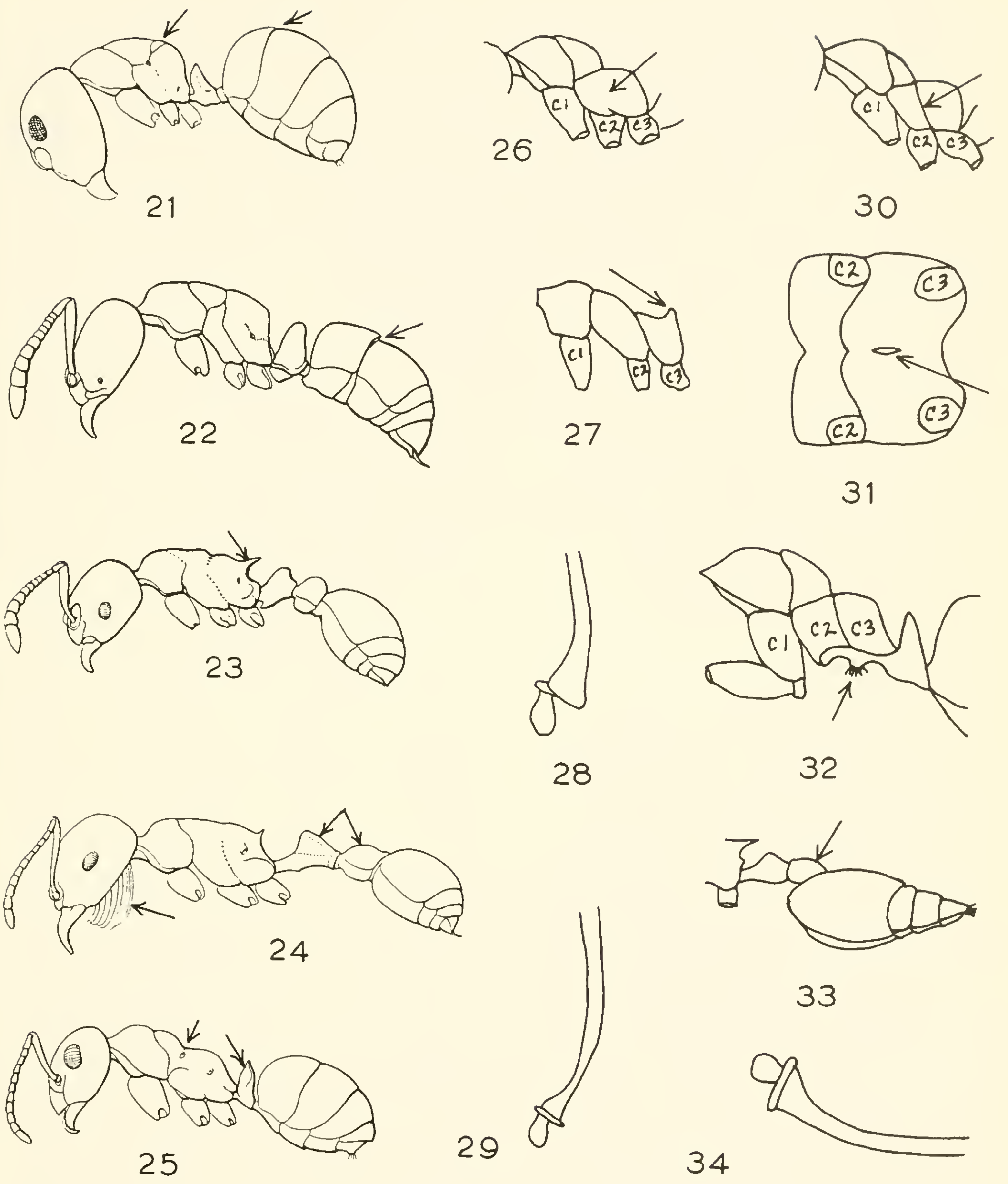
Tibia: the fourth segment of the leg (second long one from the base).

Vertex: top of head between and posterior to eyes.

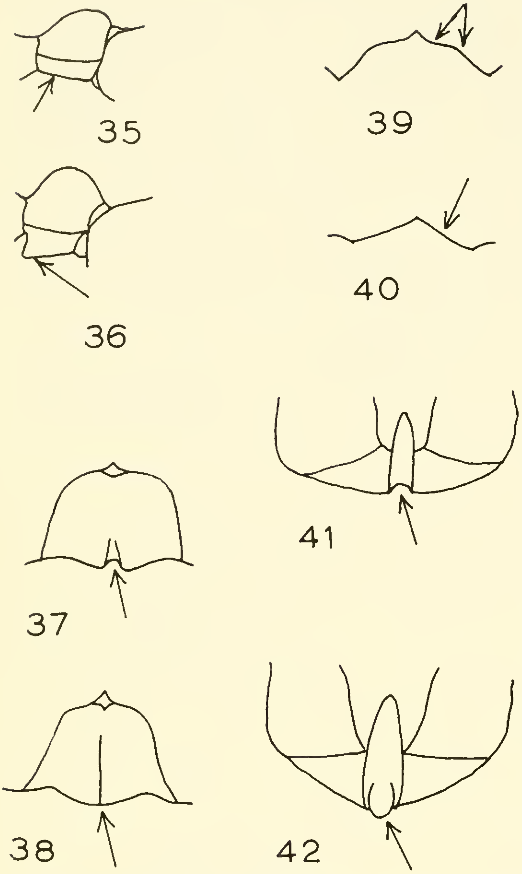
Whorls: in concentric rings.

Wrinkle (ruga): a small ridge or furrow on the surface.

Specimens in the Utah State University collection and of unpublished records of



Figs. 21–34. 21, Worker of *Camponotus sansabeanus* showing lack of constriction between 1st two segments of gaster, well-developed eye, and even convexity of thorax (from Creighton 1950); 22, Worker of *Ponera opacior* showing constriction between 1st two segments of gaster, and poorly developed eye (from Creighton 1950); 23, Worker of *Myrmica brevinodis* showing attachment of postpetiole to anterior end of gaster, and epinotal spines (from Creighton 1950); 24, Worker of *Pogonomyrmex occidentalis* showing pedicel consisting of two segments, and psammophore on underside of head (from Creighton 1950); 25, Worker of *Formica rubicunda* showing well-developed scale on pedicel of one segment, and dorsal convexity of thorax (from Creighton 1950); 26, Side of epinotum evenly curved and lacking abrupt angle; 27, Epinotum with dorsal, conical elevation; 28, Base of scape with rounded corner and poorly developed flange; 29, Base of scape thin with thin flange; 30, Side of epinotum not evenly curved, but with abrupt angle; 31, Spinasternal cavity; 32, Elevated and fringed lateral lobes of spinasternal cavity; 33, Attachment of postpetiole to dorsal surface of pointed gaster; 34, Base of scape with thick flange.



Figs. 35–42. 35, Postpetiole lacking ventral projection; 36, Postpetiole showing ventral projection; 37, Ventral median notch of clypeus; 38, Ventral margin of clypeus lacking median notch; 39, Clypeus with median flattening next to keel; 40, Clypeus with median area gradually curved to fossa; 41, Notch in apex of clypeus; 42, Anterior projection of ventral median lobe of clypeus.

George Knowlton were identified predominantly by George Wheeler, Roy Snelling, and Andre Francoeur; those in the Brigham Young University collection by Arthur Cole; and those in the University of Utah collection by Albert Grundmann and Arthur Cole. Ingham identified his own collections, and verified them by comparison with identified specimens in the University of Utah collection. I identified the ants, most of which were in the genus *Pogonomyrmex*, which I collected during my two summers of travel over Utah.

ACKNOWLEDGMENTS

I am most grateful for the unselfishness and kindness of George F. Knowlton, who loaned his personal collection records to me, which he had been accumulating for many years as a basis for a third *Ants of Utah*. He continued to periodically send me identifications of contemporary collections that he sent to Wheeler and Francoeur. Wilford Hansen, curator of the Utah State University collection, loaned all their collection and records. Mary Fors, curator of the University of Utah collection, and Albert Grundmann loaned me all their ant collections and records, and Dr. Grundmann kindly provided me with the reports of Charles Ingham on his unpublished studies of ants of southwestern Utah. George Wheeler provided records of Utah collections from his personal collection. Russell Anderson of Southern Utah State College sent their collection for identification. Andre Francoeur corrected the identification of some specimens collected by me and provided information concerning the status of some species of the large genus *Formica*. I am grateful to Brigham Young University for funds to collect ants over the state, to study collections at other universities, and for partial support of publication costs of the manuscript.

TREATMENT OF SPECIES

Under each species are listed its known collection localities in Utah, grouped by county (in boldface type), and its general distribution in the United States. Specific states of occurrence are listed only for those intermountain ones immediately adjacent to Utah (Colorado, Arizona, Nevada, Idaho, and Wyoming), which may in certain cases support some records for Utah that are questionable. In the specific locality listings for Utah, the source of the collection record is designated in parentheses for each locality, or for a series of localities listed between two record sources.

Isolated collections may be made of a species out of its normal range, elevation, or habitat. Such instances may be the result of accidental transport of winged females by directional winds or on vehicles. In most instances such individuals or small resulting colonies are not apt to survive long in unfavorable habitats. Where only one or two records are listed for the state, or its occurrence in Utah is out of place in its otherwise known range, such should be considered as temporarily questionable. Specimens representing some of these records are not available for examination; hence, the records must remain as tentative until verified by additional collections. However, one must realize that any new distribution record must always begin with one collection.

Following the Utah records, findings of other workers with reference to specific habitat, plant community relationships, and elevation are indicated. Finally, collection data taken in my study are given with pertinent field observations.

Code for Collection Locality Sources

A	Dorald M. Allred unpublished records
AC	Allred and Cole 1979
B	Buren 1968
BAD	Beck et al. 1967
BY	Brigham Young University entomology museum
C42	Cole 1942
C56	Cole 1956
C68	Cole 1968
Cr	Creighton 1950
F	Francoeur 1973
G52	Grundmann 1952
G58	Grundmann 1958
Gr63	Gregg 1963
Gr72	Gregg 1972
H	Hayward 1945
I59	Ingham 1959
I63	Ingham 1963
K70	Knowlton 1970
K75	Knowlton 1975
KU	George F. Knowlton unpublished records
O	Olsen 1934
RAU	Russell Anderson unpublished records
RG	Rees and Grundmann 1940
S73	Snelling 1973
S76	Snelling 1976
Sm52	Smith 1952
Sm53	Smith 1953
Sm57	Smith 1957
Sm79	Smith 1979
U	University of Utah entomology museum
US	Utah State University entomology museum
W67	Wheeler and Wheeler 1967
W70	Wheeler and Wheeler 1970
Wb	Weber 1947
Wi	Wilson 1955
Wg	Wing 1968
WU	George C. Wheeler unpublished records

Page Reference for Taxonomic Keys

Subfamilies 437
Genera and species of subfamily Ponerinae 438
Genera of subfamily Myrmicinae 438
  Species of Aphaenogaster 439
  Species of Crematogaster 439
  Species of Leptothorax 440
  Species of Manica 440
  Species of Myrmica 440
  Species of Pheidole 441
  Species of Pogonomyrmex 442
  Species of Solenopsis 443
  Species of Stenamma 443
Genera of subfamily Formicinae 444
  Species of Acanthomyops 444
  Species of Camponotus 445
  Species of Formica 446
  Species of Lasius 450
  Species of Myrmecocystus 451
Genera of subfamily Dolichoderinae 443
  Species of Conomyrma 444
  Species of Iridomyrmex 444

Keys to the Identification of Utah Ants

Key to Subfamilies of Formicidae Workers

(Modified by Cole 1942)

1. Pedicel of two segments (Fig. 24) 2
— Pedicel of one segment (Fig. 25) 3
2(1). Frontal carinae close together, do not cover antennal insertions (one species known from Utah, *Neivamyrmex californicus*) .... Ecitoninae
— Frontal carinae wide apart, cover antennal insertions (Fig. 3) .... Myrmicinae
3(1). Gaster constricted between first two segments (Fig. 22) .... Ponerinae
— Gaster not constricted as above (Fig. 21) 4
4(3). Anus (acidopore) terminal, circular and fringed with hairs (Fig. 13) .... Formicinae
— Anus (acidopore) subterminal and ventral, slit-shaped and not fringed with hairs (Fig. 14) .... Dolichoderinae

Key to Utah Genera and Species of Ponerinae Workers

(Modified from Creighton 1950)

1. Petiole slender, narrower dorsally than ventrally ... *Hypoponera opacior*

— Petiole robust, as wide dorsally as ventrally ... 2

2(1). Head has coarse puncta ... *Ponera pennsylvanica*

— Head has fine puncta ... *Hypoponera opaciceps*

Key to Utah Genera of Myrmicinae Workers

(Modified from Cole 1942, Creighton 1950)

1. Postpetiole attached to dorsal surface of gaster, which is flattened dorsally, convex ventrally, and acutely pointed (Fig. 33) ... *Crematogaster*

— Postpetiole attached to medioanterior or ventroanterior end of gaster, which is of usual shape, not as above (Fig. 23) ... 2

2(1). Antenna 10-segmented, has 2-segmented club (Fig. 11) ... *Solenopsis*

— Antenna has more than 10 segments; club, when developed, has more than 2 segments (Fig. 12) ... 3

3(2). Antenna 11-segmented ... 4

— Antenna 12-segmented ... 6

4(3). Thorax and petiole lack spines or teeth; pronotum never angular (one species known from Utah, *M. minimum*) ... *Monomorium*

— Epinotum has spines or teeth (Fig. 23) ... 5

5(4). Mesepinotal suture relatively deep (one species known from Utah, *F. chamberlini*) ... *Formicoxenus*

— Mesepinotal suture faint or absent ... *Leptothorax*

6(3). Laterodorsal part of clypeus elevated as a narrow ridge that forms abrupt semicircular boundary at front of antennal fossa (one species known from Utah, *T. caespitum*) ... *Tetramorium*

— Laterodorsal part of clypeus not as above ... 7

7(6). Ants of two distinct sizes, no intermediates between the extremes; antenna has a 3-segmented club that is longer than remainder of funiculus ... *Pheidole*

— Ants of several sizes, with intermediates between the extremes; antenna lacks distinct club, or, if club present, it is shorter or no longer than remainder of funiculus ... 8

8(7). Last 3 antennal segments together much shorter than remainder of funiculus, do not form an abrupt club, although they may gradually enlarge to the terminal largest segment ... 9

— Last 3 antennal segments together form an abrupt club nearly as long as remainder of funiculus ... *Leptothorax*

9(8). Dorsum of thorax has a relatively deep mesepinotal suture; psammophore absent; head, thorax and petiole sometimes with widely spaced, deep parallel wrinkles ... 10

— Dorsum of thorax lacks such a suture or at most has a slight impression; psammophore present (Fig. 24); head, thorax and petiole not as above ... *Pogonomyrmex*

10(9). Posterior tibial spurs comblike (Fig. 20) 11

— Posterior tibial spurs lack teeth 12

11(10). Epinotum has spines (Fig. 23) .... *Myrmica*

— Epinotum lacks spines .... *Manica*

12(10). Eyes small, poorly developed (Fig. 22); clypeus has 2 keels .... *Stenamma*

— Eyes large, well developed (Fig. 21); clypeus lacks keels 13

13(12). Spines of epinotum long and narrow, about as long as petiole; head not longer than broad (one species known from Utah, *V. lobognathus*) .... *Veromessor*

— Spines of epinotum short and robust, shorter than petiole; head longer than broad .... *Aphaenogaster*

Key to Utah Species of *Aphaenogaster* Workers

(Modified from Cole 1942, Creighton 1950)

1. Scape of larger workers (sometimes smaller ones) surpasses corner of head by amount less than length of 1st two funicular segments 2

— Scape of large and small workers surpasses corner of head by amount greater than length of 1st two funicular segments 3

2(1). Epinotal spines prominent; body chestnut brown .... *occidentalis*

— Epinotal spines small tubercles; head and thorax yellowish red, gaster dark brown or black .... *uinta*

3(1). Epinotum lacks teeth or spines .... *boulderensis*

— Epinotum has teeth or spines .... *huachucana*

Key to Utah Species of *Crematogaster* Workers

(Modified from Creighton 1950, Buren 1968)

1. Postpetiole lacks median groove .... *minutissima*

— Postpetiole divided by distinct median groove 2

2(1). Dorsum of thorax lacks erect hairs, or has not more than 8 confined to humeral angle of pronotum; rarely has 3 or 4 short hairs in mesepinotal suture 3

— Dorsum of thorax has at least 15 scattered erect hairs 7

3(2). Thorax densely punctate; has one or no erect hairs on humeral angle of pronotum 4

— Thorax not punctate, or, if so, has 2 or more erect hairs on humeral angle of pronotum 5

4(3). Thorax lacks erect hairs .... *depilis*

— Thorax has one erect hair on humeral angle of pronotum .... *nocturna*

5(3). Lower mesopleura has distinct striae 6

— Lower mesopleura lacks striae .... *hespera*

6(5). Head completely covered with striae and puncta .... *coarctata*

— Head smooth and shining at least behind eye, sometimes has weak impressed lines elsewhere .... *mormonum*

7(2). Hairs on thorax short, 4 or more on each pronotal shoulder, 2 or more at rear of mesonotum .... *emeryana*

— Hairs on thorax long, 1 to 3 on each pronotal shoulder; mesonotum lacks hairs .... *cerasi*

Key to Utah Species of *Leptothorax* Workers

(Modified from Creighton 1950)

1. Antenna 11-segmented 2

— Antenna 12-segmented 3

2(1). Scape has abundant erect hairs .... *hirticornis*

— Scape lacks erect hairs, or has only a few 9

3(1). Anterior part of 1st gastric tergite covered with striae and puncta .... *silvestrii*

— Anterior part of 1st gastric tergite smooth and shining 4

4(3). Posterior half of head mostly smooth and shining; broad central strip that extends forward to antennal lobes lacks sculpture .... *nitens*

— Head largely or entirely sculptured, its entire surface opaque or feebly shining 5

5(4). Dorsum of thorax densely and evenly punctate, wrinkles absent or feeble; sides of thorax have heavy puncta that obscure wrinkles 6

— Dorsum of thorax has puncta interrupted by prominent wrinkles on at least epinotum and mesonotum; wrinkles on sides of thorax not obscured by puncta 7

6(5). Epinotal spines reduced to short, stumpy angles .... *andrei*

— Epinotal spines well developed .... *nevadensis*

7(5). Scale of petiole has feeble wrinkles and dense puncta .... *furunculus*

— Scale of petiole has coarse wrinkles 8

8(7). Dorsum of thorax completely covered with coarse longitudinal wrinkles except for small heavy puncta on mesonotum .... *nevadensis*

— Wrinkles on dorsum of thorax largely confined to epinotum and rear of mesonotum; anterior prothorax has puncta only .... *tricarinatus*

9(2). Clypeus lacks ridges, its center usually flattened; mesepinotal suture present and deeply depressed 10

— Clypeus has one or more small median ridges; mesepinotal suture absent, or, if present, is not deep 11

10(9). Erect body hairs long, numerous, usually pointed .... *crassipilis*

— Erect body hairs short, sparse, usually thickened at tip .... *muscorum*

11(9). Longitudinal wrinkles of head delicate, not much coarser than sculpture between them .... *ambiguus*

— Longitudinal wrinkles of head coarse, notably heavier than sculpture between them .... *rugatulus*

Key to Utah Species of *Manica* Workers

(Modified from Creighton 1950)

1. Postpetiole has conspicuous ventral projection that extends anteriorly (Fig. 36) .... *hunteri*

— Postpetiole lacks such a projection (Fig. 35) .... *mutica*

Key to Utah Species of *Myrmica* Workers

(Modified from Cole 1942, Creighton 1950)

1. Scape gradually and evenly bent at base, upper area does not form right angle at bend (Fig. 15) 2

— Scape abruptly bent at base, upper area forms right angle (Fig. 16) 3

2(1). Lateral margin of frontal carina strongly angular above antennal insertion, thick and deflected downward toward base of antenna (Fig. 3) .... *incompleta*

— Lateral margin of frontal carina rounded and thin, deflected upward (Fig. 4) .... *brevispinosa*

3(1). Bend of scape has large, thick lobed plate that extends backward along basal third of scape (Fig. 17) .... *monticola*

— Bend of scape has small transverse plate, or thin scale, which surrounds bend like a collar and does not extend backward (Fig. 18) 4

4(3). Ventral surface of postpetiole flat or nearly so, does not form projection in front (Fig. 35) .... *americana*

— Ventral surface of postpetiole convex, or forms prominent anterior projection (Fig. 36) 5

5(4). Scale of scape forms high, semicircular welt that surrounds scape at bend .. *hamulata*

— Scale of scape not as above 6

6(5). Scale of scape small and diagonally transverse on upper surface of scape, continues as prominent transparent flange along inner surface of scape below bend .... *emeryana*

— Scale of scape not as above 7

7(6). Epinotal spines bent downward; thorax reddish yellow, head and gaster black with reddish tinge .... *emeryana*

— Epinotal spines straight, color combination not as above .... *lobicornis*

Key to Utah Species of *Pheidole* Workers

(Modified from Creighton 1950)

1. Scape of major reaches or surpasses corner of head 2

— Scape does not reach corner of head 3

2(1). Eye has more than 20 facets; head unicolored, dark brown to black .... *desertorum*

— Eye has less than 15 facets; dorsal surface of head bicolored .... *grundmanni*

3(1). Scape of major bent laterally at base toward midline of head, its flattened basal portion as wide as distal part .... *hyatti*

— Scape not bent at base, or, if slightly so, flat part at base not as wide as distal part 4

4(3). Top of head above eye and usually front face of major marked with elevations or depressions, surface opaque or feebly shining 5

— Top of head not so marked except for hair pits; surface strongly shining 7

5(4). Humeral angles of pronotum of major feebly developed, do not form lateral knobs .... *sitarches*

— Humeral angles strongly developed into epauletlike lateral knobs 6

6(5). Postpetiole of major lens-shaped, lateral projections well developed .... *pilifera*

— Postpetiole four-sided, lateral projections absent or poorly developed .... *californica*

7(4). Head of major at least 2 mm long .... *virago*

— Head of major not over 1.5 mm long 8

8(7). Sculpture on head of major extends to top of head, only the corners above the eyes smooth and shining .... *ceres*

— Sculpture largely confined to anterior half of head, all the posterior half smooth and shining 9

9(8). Mesonotum of major depressed below adjacent portion of pronotum to form distinct step or angular projection between pronotum and mesonotum .... *dentata*

— Mesonotum not so depressed, forms evenly curved outline with pronotum .... *bicarinata*

Key to Utah Species of *Pogonomyrmex* Workers

(Modified from Cole 1968)

1. Mandible has 6 teeth, the basal one much reduced; eye situated below approximate center of side of head; epinotal spines short, blunt, laterally compressed, joined posteriorly by transverse keel .... *imberbiculus*

— Mandible has 7 teeth, basal one not reduced; eye at about center of side of head; epinotal spines not as above 2

2(1). Viewed dorsally, lateral lobe of clypeus in front of base of antenna forms anteriorly-projecting broad blunt process; head much broader than long; eye small, in front view does not extend beyond side of head; 1st segment of gaster broader than long .... *rugosus*

— Viewed dorsally, lateral lobe of clypeus does not extend anteriorly; head not broader than long or only slightly so; eye large, extends beyond side of head; 1st segment of gaster not broader than long 3

3(2). Base of scape strongly enlarged, broad, its basal flange thick (Fig. 34); wrinkles on head above eye not in concentric whorls; dorsum of postpetiole not longer than broad; epinotal spines always present 4

— Base of scape weakly enlarged, its basal flange thin (Fig. 29); wrinkles of head above eye in concentric whorls; dorsum of postpetiole longer than broad; epinotal spines absent or present 7

4(3). Spaces between wrinkles on head opaque, densely and strongly punctate, producing beaded appearance 5

— Spaces between wrinkles subopaque or shining, not densely or strongly punctate, do not produce beaded appearance; spines may be reduced to tubercles .... *subnitidus*

5(4). Basal tooth of mandible offset, meets short basal mandibular margin at pronounced angle (Fig. 7), or forms a gradual curve with margin .... *occidentalis*

— Basal tooth not offset, meets long basal mandibular margin at straight angle (Fig. 6) 6

6(5). Dorsum of petiole and postpetiole has numerous strong, wavy, closely spaced, subparallel, usually transverse wrinkles; upper edge of base of scape broadly rounded, thin collar does not project beyond rounded corner (Fig. 28) .... *salinus*

— Dorsum of petiole and postpetiole not as above, but may have irregular wrinkles or lines; base of scape not broadly rounded, may be angled, thin collar projects beyond upper corner .... *owyheei*

7(3). Puncta of head and side of epinotum deep, spaces between wrinkles subopaque .... *maricopa*

— Puncta of head and thorax weak or absent; spaces between wrinkles strongly shining .... *californicus*

Key to Utah Species of *Solenopsis* Workers

(Modified from Creighton 1950)

1. 2nd segment of funiculus at least 1½ times as long as broad 2

— 2nd segment of funiculus at most only slightly longer than broad 3

2(1). Distance between eye and base of mandible 1½ times maximum diameter of eye .... *xyloni*

— Distance between eye and base of mandible at least 2 times maximum diameter of eye .... *aurea*

3(1). Puncta of head much larger in diameter than hairs that arise from them .... *salina*

— Puncta of head barely larger than hairs that arise from them .... *molesta*

Key to Utah Species of *Stenamma* Workers

(Modified from Snelling 1973)

1. Median lobe of clypeus extends beyond clypeal ventral margin, in frontal view its apex rounded or truncate (Fig. 42); eyes large, distance between eye and mandible less than 2 times eye length 2

— Median lobe of clypeus does not extend beyond clypeal anterior margin, its apex notched (Fig. 41); eye small, distance between eye and mandible more than 2 times eye length 3

2(1). Eye large, has 8–12 facets in greatest diameter .... *smithi*

— Eye small, has 6–7 facets in greatest diameter .... *chiricahua*

3(1). Frontal carinae of median lobe of clypeus subparallel or slightly divergent apically, area between carinae concave, which gives apex notched appearance 4

— Frontal carinae of clypeus strongly divergent from base, area betwen them flattened, apex not notched .... *huachucanum*

4(3). Sides of mesothorax have dense puncta; pronotal sides have coarse puncta between wrinkles .... *occidentale*

— Sides of mesothorax have coarse wrinkles; pronotal sides lack puncta between wrinkles .... *diecki*

Key to Utah Genera of Dolichoderinae Workers

(Modified from Cole 1942, Creighton 1950)

1. Scale of petiole well developed (Fig. 25) 2

— Scale of petiole vestigial or absent (one species known from Utah, *T. sessile*) .... *Tapinoma*

2(1). Epinotum has conical elevation (Fig. 27) .... *Conomyrma*

— Epinotum lacks conical elevation 3

3(2). Dorsum of thorax lacks impression at mesepinotal suture; workers of several sizes (one species known from Utah, *L. occidentale*) .... *Liometopum*

— Dorsum of thorax has slight to moderate impression at mesepinotal suture; workers of one size 4

4(3). Erect body hairs long and sparse, absent on scape and tibia .... *Iridomyrmex*

— Erect body hairs short and numerous, present on scape and tibia (one species known from Utah, *F. foetidus*) .... *Forelius*

Key to Utah Species of *Conomyrma* Workers

(Modified from Creighton 1950)

1. Head and thorax deep reddish yellow, gaster brownish black .... *bicolor*

— Color not as above .... *insana*

Key to Utah Species of *Iridomyrmex* Workers

(Modified from Creighton 1950)

1. Scape extends beyond corner of head by amount equal to or greater than length of 1st funicular segment .... *humilis*

— Scape extends beyond corner of head by amount less than length of 1st funicular segment .... *pruinosus*

Key to Utah Genera of Formicinae Workers

(Modified from Creighton 1950)

1. Antenna has 9 segments (one species known from Utah, *B. depilis*) ..... *Brachymyrmex*

— Antenna has 12 segments (Fig. 19) 2

2(1). Dorsum of thorax in profile evenly convex (Fig. 21) .... *Camponotus*

— Dorsum of thorax distinctly depressed behind level of mesonotum (Fig. 25) 3

3(2). Mandible sickle-shaped, inner border has tiny teeth (Fig. 2); maxillary palp 4-segmented, labial palp 2-segmented (one species known from Utah, *P. breviceps*) .... *Polygerus*

— Mandible triangular, inner border has large teeth (Fig. 5); maxillary and labial palps not as above 4

4(3). Maxillary palp short, 3-segmented .... *Acanthomyops*

— Maxillary palp longer, has at least 5 apparent segments (Fig. 10) 5

5(4). Psammophore present (Fig. 24); maxillary palp longer than head .... *Myrmecocystus*

— Psammophore absent; maxillary palp not longer than head 6

6(5). Frontal carinae prominent, their lateral margins slightly deflected upward; ocelli large and conspicuous .... *Formica*

— Frontal carinae poorly marked, their lateral margins flat; ocelli small and indistinct or absent 7

7(6). Scape extends past corner of head by at least one-third length of scape, usually more; erect body hairs coarse, long, usually brown or black (one species known from Utah, *P. parvula*) .... *Paratrechina*

— Scape does not surpass corner of head; erect body hairs fine, short, and golden . ... *Lasius*

Key to Utah Species of *Acanthomyops* Workers

(Modified from Wing 1968)

1. Erect hairs on dorsum of gaster segments restricted to or concentrated near posterior margins; in side profile top of scale sharp to moderately sharp; top of scale usually with median indentation .... *interjectus*

— Erect hairs on dorsum of gaster segments uniformly distributed over entire surface; scale variable in shape 2

2(1). In side profile, top of scale moderately to greatly blunt; throat has erect hairs from front to rear 3

— In side profile, top of scale moderately to greatly sharp; throat has erect hairs only on one-half to three-fourths of posterior surface 4

3(2). Erect hairs more numerous on dorsum of epinotum than on pro- and mesothorax; 1st femur has 10 or less erect hairs; scape lacks erect hairs .... *murphyi*

— Erect hairs about evenly distributed over entire dorsum of thorax; 1st femur has 12 or more erect hairs; scape may have or lack erect hairs .... *latipes*

4(2). Side of 2nd segment of gaster densely covered with hairs, the distance between hairs less than one-third their length; appendages and most of body densely covered with hairs .... *occidentalis*

— Side of 2nd segment of gaster moderately to thinly covered with hairs, the distance between hairs more than one-half their length; appendages and body moderately to thinly covered with hairs 5

5(4). Body color yellow; erect hairs on throat 0.13 mm or more in length, those on gaster 0.18 mm or more; hairs delicate .... *creightoni*

— Body color yellowish brown to brown; erect hairs on throat 0.12 mm or less in length, those on gaster 0.17 mm or less; hairs coarse .... *coloradensis*

Key to Utah Species of *Camponotus* Major Workers

(Modified from Creighton 1950, Gregg 1963)

1. Ventral border of clypeus depressed in middle to form thin anterior edge, usually with narrow median notch (Fig. 37); clypeus usually has short triangular depression behind notch 2

— Ventral border of clypeus not depressed, edge wide, sometimes with notch; short triangular depression absent 5

2(1). Mesepinotal suture broadly impressed, involves rear of mesonotum and front of epinotum .... *hyatti*

— Mesepinotal suture not impressed, or, if slightly so, only as groove on front of epinotum 3

3(2). Corner of head strongly shining, sides of head notably narrowed at level of mandibles .... *essigi*

— Corner of head opaque or feebly shining, sides of head not unusually narrowed at level of mandibles 4

4(3). Clypeus much broader than long .... *nearcticus*

— Clypeus only slightly broader than long .... *rasilis*

5(1). Clypeus lacks distinct ridge or keel, but sometimes has slight one; scape not flattened at base; head broader than long 6

— Clypeus has distinct ridge or keel, sometimes reduced; if reduced, scape flattened at base; head as long as or longer than broad 9

6(5). Scape has scattered erect hairs; entire ant jet black and shining, often with bluish reflections .... *laevigatus*

— Scape lacks erect hairs except for small cluster at extreme tip; color not as above, but if black then not shining and lacks bluish luster 7

7(6). Scape reaches only to or barely extends beyond corner of head .... *herculeanus*

— Scape extends beyond corner of head by amount greater than maximum diameter of scape 8

8(7). Pubescence on gaster absent or fine and sparse; entire surface of gaster shining ..... *novaeboracensis*

— Pubescence on gaster coarse and relatively dense, surface dull except for narrow lighter-colored band at posterior edge of each segment ..... *modoc*

9(5). Scape extends beyond corner of head by amount equal to or greater than length of 1st funicular joint 10

— Scape does not extend beyond corner of head, or, if so, by amount less than length of 1st funicular joint ..... *sansabeanus*

10(9). Scape distinctly flattened at base, flattened portion forms small lateral lobe ..... *semitestaceus*

— Scape not flattened at base, or, if flattened, lacks lateral lobe 11

11(10). Cheek strongly shining, has tiny inconspicuous puncta ..... *ocreatus*

— Cheek dull or feebly shining, has coarse and conspicuous puncta ..... *vicinus*

Key to Utah Species of *Formica* Workers

(Modified from Creighton 1950, Francoeur 1973, Wheeler and Wheeler 1977)

1. Ventral margin of clypeus has median notch (Fig. 37); short hairs on gaster dense; body bicolored with head and thorax reddish brown or reddish yellow, gaster brown or black; in side profile dorsomedian area of the epinotum between mesoepinotal suture and petiole angled, not broadly curved 2

— Lacks above combination of characters (Fig. 38) 10

2(1). Dorsum of 1st segment of gaster strongly shining, its thin hairs do not obscure delicate rough sculpture 3

— Dorsum of 1st segment of gaster opaque or feebly shining, its dense hairs partially obscure fine leatherlike sculpture 4

3(2). Basal face of petiole has many long erect hairs; other body hairs long and numerous ..... *perpilosa*

— Basal face of petiole lacks long erect hairs, or has cluster of short erect ones near junction with sloping face; other body hairs short and not abundant ..... *manni*

4(2). Dorsum of thorax lacks erect hairs, or has few fine short inconspicuous ones only on pronotum 5

— Dorsum of pronotum and mesonotum has conspicuous erect hairs 8

5(4). In front face view of largest workers, outer margin of eye reaches or surpasses margin of head 6

— In front face view of largest workers, distinct space evident between outer margin of eye and margin of head 7

6(5). Scape slender, not thickened at tip; basal face of epinotum lacks transverse impression ..... *pergandei*

— Scape robust, tip thickened; basal face of epinotum has distinct transverse impression ..... *emeryi*

7(5). Scale of petiole has blunt crest; gaster plain brown; upper face of epinotum at right angle to base ..... *subintegra*

— Scale of petiole has sharp crest; gaster blackish brown; upper face of epinotum at greater than right angle to base ..... *subnuda*

8(4). Gaster has long, stout, silvery, erect hairs blunt at tip; erect hairs on other parts of body about as abundant as those on gaster ..... *obtusopilosa*

— Erect hairs on gaster yellow, not blunt at tip; erect hairs on other parts of body much more sparse than on gaster 9

9(8). Scape has abundant suberect hairs, those on inner surface near tip distinctly erect ..... *puberula*

— Scape lacks suberect or erect hairs ..... *wheeleri*

10(1). From posterior profile, upper surface of side of epinotum evenly curved to base (Fig. 26); body surface shining 11

— From posterior profile, upper surface of side of epinotum angled before its base (Fig. 30); body surface dull 14

11(10). Scale more than 1¼ length of head; frontal carinae diverge dorsally; posterior face of petiole scale convex ..... *pallidefulva*

— Scape less than 1¼ length of head; frontal carinae subparallel, do not diverge dorsally; posterior face of petiole scale not convex 12

12(11). Scape has short, delicate, whitish, erect hairs ..... *lasioides*

— Scape lacks erect hairs except for small cluster at extreme tip 13

13(12). Thorax has numerous erect hairs ..... *neogagates*

— Thorax lacks erect hairs, or has only 1 or 2 ..... *limata*

14(10). Dorsal border of head of larger workers strongly concave; pronotum in profile angled between base and upper surface ..... *opaciventris*

— Dorsal border of head of larger workers straight or only slightly concave; pronotum in profile evenly convex 15

15(14). Erect hairs on pronotum distinctly broader at tip than at base 16

— Erect hairs on pronotum absent, or, if present, taper from base to pointed tip or of equal width throughout their length 20

16(15). Tibia has erect or suberect hairs in addition to double row on flexor surface; scape hairs variable, often erect ..... *microgyna*

— Tibia lacks erect hairs except for double row on flexor surface; scape lacks erect hairs except for few at extreme tip 17

17(16). Dorsal border of head evenly convex ..... *querquetulana*

— Dorsal border of head flat or concave 18

18(17). Crest of petiole lacks erect hairs; pubescence on dorsum of gaster thin, does not wholly conceal surface at rear edges of segments ..... *whymperi*

— Crest of petiole has erect hairs; pubescence on dorsum of gaster dense, wholly conceals surface 19

19(18). Erect hairs on dorsum of head and thorax sparse, or inconspicuous or absent ..... *rasilis*

— Erect hairs on dorsum of head and thorax abundant and conspicuous ..... *densiventris*

20(15). Body bicolored with head and thorax reddish or yellowish red, both lighter than dark gaster; front of head shining; frontal carinae strongly divergent 21

— Body unicolored or bicolored—if bicolored then only thorax lighter than gaster; front of head opaque; frontal carinae parallel or moderately divergent dorsally 33

21(20). Scape has numerous delicate erect or suberect hairs ..... *oreas*

— Scape lacks erect hairs except at extreme tip, or has few scattered on inner surface near tip 22

22(21). In ventral profile, median face of clypeus on each side of keel almost flattened to form abrupt curve or angle between keel and fossa (Fig. 39) 23

— In ventral profile, upper face of clypeus not flattened, face forms a gradual curve from keel to fossa (Fig. 40) 25

23(22). Middle and hind tibiae lack erect hairs except for double row of bristles on flexor surface 24

— Middle and hind tibiae have many erect hairs in addition to double row of bristles .... *obscuriventris*

24(23). Upper surface of body lacks erect hairs; gaster pubescence thin, surface strongly shining .... *fossaceps*

— Upper surface of body has abundant erect hairs; gaster pubescence dense, whitish, surface opaque .... *laeviceps*

25(22). Middle and hind tibiae have many erect hairs on all surfaces besides bristles on flexor surface 26

— Middle and hind tibiae lack or rarely have 1 or 2 erect hairs other than bristles on flexor surface 27

26(25). Head of major as broad as or broader than long; erect hairs on thorax unequal in length .... *obscuripes*

— Head of major longer than broad; erect hairs on thorax short and about equal in length .... *subnitens*

27(25). Gaster densely covered with short erect hairs of plushlike appearance viewed in profile 28

— Erect hairs of gaster widely spaced, not plushlike in profile 30

28(27). Throat lacks erect hairs, or has 1 or 2 suberect ones .... *ciliata*

— Throat has several to 12 or more erect hairs 29

29(28). Erect hairs on gaster short, average about 0.06 mm .... *comata*

— Erect hairs on gaster long, average about 0.12 mm .... *mucescens*

30(27). Mid and hind tibiae lack row of bristles but have 3 or 4 near spur .... *criniventris*

— Mid and hind tibiae have row of erect bristles that extend for one-half length or more of tibiae 31

31(30). Head of largest worker as broad as long .... *obscuripes*

— Head of largest worker longer than broad 32

32(31). Throat, crest of petiole, and dorsum of thorax lack erect hairs, sometimes few present .... *haemorrhoidalis*

— Throat, crest of petiole, and dorsum of thorax have numerous erect hairs, sometimes throat and petiole have only 1 or 2 .... *integroides*

33(20). Metasternum has 2 distinct hairy lobes that arise on each side of spinasternal cavity (Figs. 31, 32) 34

— Metasternum lacks such lobes 42

34(33). Head and body of uniform color 35

— Head and body each bicolored 39

35(34). Dark brown or black 36

— Pale brown or yellowish brown 38

36(35). Throat lacks erect hairs .... *occulta*

— Throat has erect hairs 37

37(36). Cheek and side of prothorax have erect hairs .... *canadensis*

— Cheek and side of prothorax lack erect hairs .... *altipetens*

38(35). Throat lacks erect hairs .... *neoclara*

— Throat has erect hairs .... *canadensis*

39(34). Throat lacks erect hairs .... *neoclara*

— Throat has erect hairs 40

40(39). Yellowish brown to brownish black; gaster darker than head, which is darker than thorax; head of largest worker as broad as long; gaster pubescence thin, surface strongly shining .... *subpolita*

– Gaster and upper portion of head yellowish brown to dark brown, thorax and lower part of head paler; head of largest worker longer than broad; gaster pubescence normal or dense, surface opaque or feebly shining 41

41(40). Corner of head and side of prothorax have erect hairs .... *canadensis*

— Corner of head and side of prothorax lack erect hairs .... *altipetens*

42(33). Head and body of uniform color 43

— Head and body each bicolored 52

43(42). Dark brown or black 44

— Pale brown or yellowish brown 51

44(43). Cheek between eye and mandible has coarse, elongate puncta widely spaced on upper half .... *hewitti*

— Cheek between eye and mandible lacks coarse, elongate puncta, or, if present, concentrated mostly on upper half 45

45(44). Throat lacks erect hairs 46

— Throat has erect hairs 50

46(45). Hairs on dorsum of 1st segment of gaster (exclusive of posterior row) usually more than 10; spinasternal cavity not surrounded by hairs (Fig. 31) 48

— Hairs on dorsum of 1st segment of gaster (exclusive of posterior row) less than 10; spinasternal cavity surrounded by hairs 47

47(46). Length of scape greater than length of head; anterior margin of clypeus angled .... *accreta*

— Length of scape less than length of head; anterior margin of clypeus broadly convex .... *fusca*

48(46). Cheek and dorsum of 1st 4 segments of gaster have dense pubescence producing a silvery luster .... *argentea*

— Cheek and dorsum of 1st 4 segments of gaster have normal to thin pubescence, not silvery, but may have silky luster 49

49(48). Length of scape shorter than length of head; sides of head only slightly rounded, diverge toward base of mandibles; posterior margin of head straight or slightly convex .... *podzolica*

— Length of scape equal to or longer than length of head; sides of head broadly rounded; posterior margin of head strongly convex .... *subsericea*

50(45). Length of scape greater than length of head; scale of petiole has dorsal median notch .... *transmontanis*

— Length of scape not greater than length of head; scale of petiole not notched ... . *aerata*

51(43). Throat has erect hairs .... *aerata*

– Throat lacks erect hairs .... *argentea*

52(42). Throat has erect hairs 53

– Throat lacks erect hairs 54

53(52). Cheek between eye and mandible has coarse, elongate puncta, widely spaced on upper half .... *hewitti*

– Cheek between eye and mandible lacks coarse, elongate puncta, or, if present, concentrated on upper half .... *aerata*

54(52). Cheek between eye and mandible has coarse, elongate puncta, widely spaced on upper half .... *neorufibarbis*

– Cheek between eye and mandible lacks coarse, elongate puncta, or, if present, concentrated on upper half 55

55(54). Epinotum high with distinct angle .... *gnava*

– Epinotum long and low with even convexity .... *xerophila*

Key to Utah Species of *Lasius* Workers

(Modified from Wilson 1955)

1. Eye length 0.2 times or more width of head 2

– Eye length 0.17 times or less width of head 6

2(1). Mandible has one or more offset teeth at basal angle (Fig. 5) .... *pallitarsus*

– Basal tooth of mandible aligned with adjacent teeth (Fig. 6) 3

3(2). Scape lacks erect hairs; eye length usually less than 0.25 times width of head; color yellowish brown .... *sitiens*

– Scape has erect hairs; eye length more than 0.25 times width of head; color other than yellowish brown 4

4(3). Next to last basal tooth of one or both mandibles markedly reduced in size relative to 2 flanking teeth, or gap between next to last and last basal teeth larger than last basal tooth .... *crypticus*

– Next to last basal tooth subequal in size or larger than last basal tooth, gap between them about same as last tooth 5

5(4). Scape and tibia have less than 10 or lack erect or suberect hairs .... *alienus*

– Scape and tibia have more than 10 erect or suberect hairs .... *niger*

6(1). In frontal or posterior view, dorsal crest of petiole strongly convex and not notched .... *humilis*

– Dorsal crest of petiole truncate or slightly convex, often notched 7

7(6). Eye has less than 35 facets 8

– Eye has 35 or more facets 9

8(6). Outer surface of tibia has numerous erect or suberect hairs .... *fallax*

– Outer surface of tibia has only 1 or 2 erect or suberect hairs .... *nearcticus*

9(7). Longest hairs of posterior half of dorsum of 1st segment of gaster (exclusive of extreme posterior strip) not longer than one-half maximum width of hind tibia at midlength .... *umbratus*

– Longest hairs situated as above at least three-fifths as long as tibia width 10

10(9). Posterior half (except extreme posterior strip) of dorsum of 1st segment of gaster has hairs no more than semierect; erect hairs on tibia absent or sparse .... *subumbratus*

— Posterior half (except extreme posterior strip) of dorsum of 1st segment of gaster has erect hairs; erect hairs on tibia abundant .... *vestitus*

Key to Utah Species of *Myrmecocystus* Workers

(Modified from Snelling 1976)

1. Mandible has 8 to 10 teeth; integument light yellow or brownish yellow; ocelli absent or much reduced 2

— Mandible has 6 or 7 teeth; integument not as above, but rusty red brown, black, orange or combination; ocelli well developed 5

2(1). Dorsal surface of epinotum strongly projected upward over posterior two-thirds; erect hairs sparse; upper margin of eye barely below upper margin of head .... *pyramicus*

— Dorsal surface of epinotum flat or evenly convex; body often abundantly hairy; upper margin of eye well below upper margin of head 3

3(2). Head, pronotum, and gaster shiny, have few if any nonerect hairs; mid and hind tibiae have no more than 3 or 4 erect hairs beyond basal third of outer face; mesepinotal suture deeply impressed .... *navajo*

— Head, pronotum, and gaster abundantly hairy; mid and hind tibiae have numerous erect hairs; mesepinotal suture not deeply impressed, but, if so, head length exceeds 1.3 mm 4

4(3). Mesepinotal suture impressed; epinotum as long as or longer than high, juncture of dorsal and posterior faces broadly rounded .... *mexicanus*

— Mesepinotal suture not impressed; epinotum higher than long, juncture abruptly rounded or slightly angular .... *testaceus*

5(1). Uniform blackish or dark brown; anterior one-third of head may be paler; hairs on head sparse, with few erect hairs .... *hammettensis*

— Bicolored or rusty red brown; head has abundant hairs, many of them erect 6

6(5). 20 or more erect hairs on cheek in front view; scape, femur, and tibia have numerous suberect hairs on all surfaces .... *mendax*

— Less than 20 erect hairs on cheek; scape and femur have sparse suberect hairs 7

7(6). Cheek in frontal view has 6 or more erect hairs evenly distributed between eye and base of mandible 8

— Cheek in frontal view has no more than 4 erect hairs confined to lower half near mandible 10

8(7). Erect hairs present over at least one-half distance between inner margin of eye and base of antenna; puncta of face irregularly distributed .... *semirufus*

— Erect hairs present only adjacent to inner margin of eye, do not extend more than one-fourth distance between eye and antennal base; puncta of face evenly distributed 9

9(8). Longest pronotal hairs more than one-half length of minimum diameter of eye; cheek usually has 12 to 16 erect hairs; top of head finely punctate toward sides .... *romainei*

— Longest pronotal hairs less than one-half diameter of eye; cheek usually has fewer than 12 erect hairs; top of head not punctate .... *flaviceps*

10(7). Dorsum of segment 3 of gaster has dense short hairs .... *flaviceps*

— Dorsum of segment 3 of gaster has few or no short hairs 11

11(10). Face has sparse short hairs; head shiny; head, thorax, and legs brownish .... *mimicus*

— Face has abundant hairs; head not shiny; head, thorax, and legs rusty red brown .... *kennedyi*

Acanthomyops coloradensis (Wheeler)

Lasius interjectus coloradensis Wheeler, 1917, Proc. Amer. Acad. Arts, Sci. 52:532.

L. claviger: Rees and Grundmann 1940:7; Cole 1942:375.

A. coloradensis: Wing 1968:79; Smith 1979:1441.

Records: **SALT LAKE**: Lake Blanche (RG). **SAN JUAN**: locality unknown (Wg68). **UINTAH**: Vernal 13.4 mi NW (A). **WASATCH**: Francis 14.4 mi E, Soldier Summit 3.3 mi N (A).

Smith (1979:1441) lists this species from western United States, including Utah and Colorado. Most colonies have been found under stones. Gregg (1963:484) lists it in Colorado between 4654 and 8000 ft under rocks in conifers, oak, grass, and other habitats. Wing (1968) lists it from Arizona with an altitudinal range of 2000 to 7000 ft. Three elevational records for Utah are 4750, 7100, and 7463 ft.

Acanthomyops creightoni Wing

A. creightoni Wing, 1968, Cornell Univ. Agric. Expt. Sta., Mem. 405:141; Smith 1979:1441.

Record: **GRAND**: Warner Ranger Sta (Wg68).

Smith (1979:1441) lists this species only from Utah. One elevational record is 9750 ft.

Acanthomyops interjectus (Mayr)

Lasius interjectus Mayr, 1866, Zool.-Bot. Ges. Wien, Verh. 16:888; Rees and Grundmann 1940:7; Cole 1942:375.

A. interjectus: Ingham 1959:75; Wing 1968:95; Smith 1979:1441.

A. claviger: Beck et al. 1967:68.

Records: **IRON**: Cedar City (RG). **JUAB**: Joy (BAD). **KANE**: locality unknown (Wg68). **SALT LAKE**: Big Cottonwood Cyn (C42).

Smith (1979:1441) lists this species from eastern to western United States, including Utah and Idaho, where it occurs mainly in woodlands, pastures, or meadows in exposed soil sometimes mounded, or under stones or logs. Gregg (1963:484) lists it from Colorado between 5200 and 8700 ft under rocks and logs in a variety of habitats. Wing (1968) lists it from Arizona. Cole (1942:375) indicates its habitat in Utah as under stones, one collection known at 10,000 ft. Ingham (1959) found it under stones in southern Utah. Wheeler and Wheeler (1977) found it in North Dakota most frequently under rocks. Two elevational records for Utah are 5800 and 5834 ft. Beck et al. (1967:68) found it feeding on a dead pocket mouse in one instance in Utah.

Acanthomyops latipes (Walsh)

Formica latipes Walsh, 1862, Proc. Ent. Soc. Phila. 1:311.

Lasius latipes: Rees and Grundmann 1940:7; Cole 1942:375.

A. latipes: Wing 1968:101.

Records: **CACHE**: Logan (C42). **CARBON**: Spring Cyn (City) (C42) (=Storrs). **DUCHESNE**: Blue Bench (C42), Currant Crk (US). **GARFIELD**: locality unknown (Wg68). **IRON**: locality unknown (Wg68). **SALT LAKE**: locality unknown (RG). **SAN JUAN**: Monticello (RG). **SANPETE**: Majors Flats (KU). **UTAH**: Aspen Grove (BY). **WASATCH**: Currant Crk (C42).

Smith (1979:1441) lists this species from eastern to western United States, including Arizona, where it occurs in open woodlands, meadows, or pastures in earthen mounds, or under stones or at the base of stumps. Gregg (1963:486) lists it from Colorado between 4800 and 8500 ft under rocks in a variety of habitats. Wing (1968) lists it from Arizona. Cole (1966:20) found its nests under stones in pinyon-juniper in southern Nevada. Wheeler and Wheeler (1963) found it frequently under rocks in North Dakota.

One hundred thirty ants in three colonies in Utah were under rocks. Three collections were in sagebrush: one with matchbrush, one with snowberry, and one at the edge of aspen.

Acanthomyops murphyi (Forel)

Lasius murphii Forel, 1901, Ann. Soc. Ent. Belg. 45:367.

A. murphyi: Wing 1968:115; Smith 1979:1441.

Records: **DUCHESNE**: locality unknown (Wg68). **SAN JUAN**: locality unknown (Wg68).

Smith (1979:1441) designates this species as eastern to western United States, including Utah and Idaho, where it nests under stones in open woodlands. Gregg (1963:490) lists it from Colorado between 5354 and 7200 ft under rocks in several habitats. Wing (1968) lists it from Arizona.

Acanthomyops occidentalis (Wheeler)

Lasius occidentalis Wheeler, 1909, J. New York Ent. Soc. 17:83.

A. occidentalis: Wing 1968: 124; Wheeler and Wheeler 1977; Smith 1979:1442.

Record: **UINTAH**: locality unknown (Wg68).

Smith (1979:1442) lists this species from midwestern and western United States, including Utah, Colorado, and Wyoming. Wing (1968) lists it from Arizona under stones.

Aphaenogaster boulderensis M.R. Smith

A. boulderensis Smith, 1941, Great Basin Nat. 2:120; Ingham 1959:47.

Aecords: **WASHINGTON**: St. George, Zion Nat Park (I59).

Smith (1979:1360) lists two subspecies from the western United States, including Arizona and Nevada, probably nesting under stones. The population in Utah is likely *A. b. boulderensis*. Cole (1966:9) found it in southern Nevada in mixed desert shrubs. Ingham (1963) found it in blackbrush in southern Utah. Eight elevations for Utah are between 2500 and 7066 ft.

Aphaenogaster huachucana Creighton

A. huachucana Creighton, 1934, Psyche 41:189; Ingham 1959:48.

Record: **IRON**: New Harmony (I59).

Smith (1979:1361) lists two subspecies from western United States, including Colorado and Arizona. The race in Utah is likely *A. h. huachucana*. Gregg (1963:340) lists it between 5100 and 6300 ft under rocks in pinyon-juniper-oak areas in Colorado. Ingham (1959) found it under rocks in juniper, pinyon, sagebrush, and oak in southern Utah. Two elevation records for Utah are 5250 and 6000 ft.

Aphaenogaster occidentalis (Emery)

Stenamma subterraneum occidentale Emery, 1895, Zool. Jahrb. Syst. 8:301.

A. subterranea occidentalis: Rees and Grundmann 1940:4; Cole 1942:364; Beck et al. 1967:68.

A. subterranea valida: Creighton 1950:150; Ingham 1959:49; Beck et al. 1967:68; Smith 1979:1362.

Records (Map 1): **BOX ELDER**: Box Elder Cyn (US), Brigham (C42), Locomotive Spngs (BAD), Mantua Mt (C42). **CACHE**: Blacksmith Fk Ranger Sta (BAD), Franklin Basin (KU), Green Cyn, Hyde Park (US), Logan, Logan Cyn, Providence Cyn (C42), Wellsville Cyn (US). **DAVIS**: Muellers Cyn (U). **GRAND**: Thompson (C42). **IRON**: Cedar City 7 mi E (A), Summit Crk (RAU). **JUAB**: Eureka 0.5 mi E, Nebo Loop Rd 9.9 mi S Santaquin Cyn, Ponderosa Cmpgnd (A). **MILLARD**: Oak Crk Cyn (US). **MORGAN**: Morgan (BAD). **RICH**: Chalk Crk (U). **SALT LAKE**: Big Cottonwood Cyn, Butterfield Cyn, S Dry Cyn, Ft Douglas, Holliday (C42), Little Willow Cyn (RG), Mt Olympus, Red Butte Cyn (U), Salt Lake City (RG), Univ Utah Campus (C42). **SAN JUAN**: Abajo Mts (U). **SANPETE**: Fountain Green 3 mi W (A), Majors Flats (KU). **TOOELE**: S Willow Cyn (U). **UTAH**: American Fk Cyn (U), Provo (A), N Fk Provo Cyn (U), Santaquin 3.6 and 4.6 mi E (A), Spanish Fk Cyn (KU), Thistle 2.7 and 20.4 mi E (A). **WASATCH**: Midway 3.7 mi NW and 5.7 mi W (A), Soapstone Cyn (U). **WASHINGTON**: Pine Valley (City) (BAD), Zion Nat Park (I59). **WEBER**: Woodruff 34.8 mi W (A).

Creighton (1950) and Smith (1979:1362) list two subspecies as occurring in the western United States, including Utah, Colorado, and Nevada, where they nest under stones in foothill canyons. Both races have been recorded from Utah, and may be separated as follows. Largest workers of *valida* are 6 mm in length and are bright red brown, whereas *occidentalis* workers are only 4.5 mm and are blackish brown. Gregg (1963:344) lists this species between 5354 and 7500 ft under rocks and logs predominantly in oak and deciduous areas in Colorado. Hunt and Snelling (1975:21) list it from Arizona. Wheeler and Wheeler (1978:391) found it between 5200 and 8400 ft in Nevada. Cole (1942:364) indicates its habitats in Utah as under stones and in ditch banks. Ingham (1959) lists its habitat as under stones and logs in pinyon-juniper, oak, sagebrush, and ponderosa pine in southern Utah.

There were 374 ants of 11 colonies under rocks. One colony was under the same rock as a colony of *Lasius pallitarsus*. Seven ants were attracted to a can containing meat juices. Six colonies were in grass: one with herbs and sagebrush; one with herbs, sagebrush, and rabbitbrush; one herbs, maple, and oak; two serviceberry, maple, and oak; and one maple and oak. Two colonies were in sagebrush, one in fir, two in oak, one in fir and oak, and one in mahogany. In 51 recorded Utah habitats it occurred 34 times in canyons above 5000 ft. In 27 collections where the elevation was known, it occurred about equally between 4253 and 7700 ft. One collection was at 9000. Eggs were found in late June and early July, and larvae in late June.

In one instance, when the cover rock was removed, these ants attempted to carry the exposed larvae into their burrow. In another instance, when ants of a nearby *Formica integroides* colony periodically crawled into the home range area of *subterranea*, these latter ants quickly entered their burrow. Beck et al. (1967:68) found it feeding on dead mice in four instances in Utah.

Aphaenogaster uinta Wheeler

A. uinta Wheeler, 1917, Proc. Amer. Acad. Arts Sci. Boston 52:517; Rees and Grundmann 1940:4; Cole 1942:364; Creighton 1950:154; Ingham 1963:77; Knowlton 1970:208, 1975:2; Smith 1979:1363.

Records (Map 1): **BOX ELDER**: Dolphin Island (in Great Salt Lake) (C42), NW Kelton (K75) and 9 mi N (K70). **DUCHESNE**: NW Roosevelt (KU); **EMERY**: Goblin Valley 10 mi E (KU). **IRON**: SE Lund (I63). **JUAB**: Chicken Crk Res (KU), Eureka 0.5 mi E (A). **SALT LAKE**: Big Cottonwood Cyn (U), S Dry Cyn (C42), E Mill Crk Cyn (RG), Point-of-Mt (C42), Salt Lake City (RG).

Smith (1979:1363) lists this as a western intermountain species, including Utah, Colorado, Nevada and Idaho, where it nests in fully exposed, dry areas. Cole (1942:364) indicates its nests as under stones in Utah. Ingham (1963) found it in alkali flats in southern Utah.

Forty ants of one colony were in grass, herbs, and sagebrush under a rock. In 13 recorded Utah habitats it occurred only 3 times in montane areas. In 7 recorded elevations between 4253 and 6425 ft, 5 were between 5000 and 5500.

Brachymyrmex depilis Emery

B. heeri depilis Emery, 1893, Zool. Jahrb. Syst. 7:635.
B. depilis flavescens: Grundmann 1952:117.

Records: **BOX ELDER**: Wellsville Mts (KU). **SALT LAKE**: Big Cottonwood Cyn (G52).

Smith (1979:1424) lists this species as mainly eastern United States, nesting under stones and wood. He does not list an intermountain state. Gregg (1963:449) lists it from Colorado between 4600 and 7000 ft under rocks in conifers, oak, and deciduous habitats. Wheeler and Wheeler (1963) found it frequently under rocks in North Dakota.

Camponotus essigi M.R. Smith

C. caryae var. *essigi* Smith, 1923, Ent. News 24:306.

Records (Map 2): **BOX ELDER**: Hansel Mts, Mantua (KU).

Smith (1979:1432) lists this species as western United States, including Nevada and Idaho. Hunt and Snelling (1975:22) list it from Arizona. Wheeler and Wheeler (1978:393) found it between 6000 and 7800 ft in Nevada. One Utah elevational record is 5175 ft.

Camponotus herculeanus (Linnaeus)

Formica herculeana Linnaeus, 1758, Syst. Nat. Ed. 10, 1:579.
C. herculeanus whymperi: Rees and Grundmann 1940:11; Cole 1942:388; Hayward 1945:120.
C. herculeanus: Smith 1979:1426.

Records (Map 3): **CACHE**: Logan (KU), Logan Cyn (US), Monte Cristo (KU). **CARBON**: Scofield (BAD). **DAVIS**: Mueller Park (C42). **DUCHESNE**: Duchesne 30 mi SW (US), Mirror Lake (U), Roosevelt (C42). **GARFIELD**: Bryce Cyn Nat Park (US). **JUAB**: Nephi 5.5 mi W (A). **RICH**: Garden City, Meadowville (KU). **SALT LAKE**: Brighton (U), Cottonwood, Draper (US), Lake Blanche (C42), Red Butte Cyn (U). **SAN JUAN**: Monticello 9.5 mi W (A). **SANPETE**: Bluebell Flats, Ephraim Cyn (KU), Maple Cyn (U), Mt. Pleasant, Pleasant Crk (BAD). **SUMMIT**: Henrys Fk (RG), Kamas 11 mi E (U). **UINTAH**: Whiterocks Cyn (KU). **UTAH**: Aspen Grove (BY), Provo (U), Santaquin 6.7 mi E (A). **WASATCH**: Horse Crk (C42), Midway 11.6 mi W (A), N Fk Provo River (U). **WEBER**: Uintah (US).

Smith (1979:1426) lists this species as eastern to western United States, including Utah and Colorado, where it nests in rotting logs and stumps primarily in montane forest. Gregg (1963:658) lists it between 5150 and 12,500 ft under rocks and logs predominantly in conifer habitats in Colorado. Cole (1942:388) indicates its habitats as logs and stumps, particularly conifers, at high elevations in Utah.

One ant was taken singly in the open, three under a log, and five under a rock. Specimens were found in grass, sagebrush, and oak; chokecherry and aspen; junipers and conifers. In 33 recorded Utah habitats it occurred 20 times in montane forest. In 15 recorded elevations between 4490 and 10,050 ft, it occurred most frequently under 6000. When disturbed by removal of their covering these ants quickly hide.

Camponotus hyatti Emery

C. hyatti Emery, 1893, Zool. Jahrb. Syst. 7:669.

Record (Map 2): **CACHE**: Green Cyn (KU).

Smith (1979:1432) lists two subspecies as western United States, including Nevada, where they nest in the soil or in or under dead limbs. The Utah race is likely *hyatti*, which may be differentiated by its entire black or dark brown gaster, whereas in *bakeri* the basal two-thirds of the 1st gastric segment is red. Cole (1966:19) found one nest under a juniper log in mixed brush in a desert area in southern Nevada.

Camponotus laevigatus (F. Smith)

Formica laevigata Smith, 1858, Cat. Hym. Brit. Mus. 6:55.

C. laevigatus: Rees and Grundmann 1940:11; Cole 1942:388; Ingham 1959:70.

Records (Map 2): **BEAVER**: Beaver Cyn (RG). **CACHE**: Logan, Logan Cyn (C42). **GARFIELD**: Carcass Crk on Boulder Mt (U). **GRAND**: La Sal Mts (BY). **IRON**: Cedar City 7 mi E (159). **SAN JUAN**: Monticello 18.5 mi E (U), Navajo Mt (US). **UTAH**: Aspen Grove (C42), Provo (BY). **WASATCH**: Kamas 11 mi SE (U). **WASHINGTON**: Pine Valley (City) (159), Zion Nat Park (BY). **WAYNE**: Boulder Mt (US).

Smith (1979:1426) lists the distribution of this species as western United States, including Colorado, where it nests in logs and stumps in forested areas. Hunt and Snelling (1975:22) list it from Arizona. Gregg (1963:662) lists it between 5354 and 8700 ft under logs predominantly in conifer habitats in Colorado. La Rivers (1968:7) lists it from Nevada, where Wheeler and Wheeler (1978:392) found it between 6400 and 8600 ft. Cole (1942:388) indicates its habitat as dry logs in open woods in Utah. Ingham (1959) found it in logs in ash, willow, poplar, oak, and ponderosa pine in southern Utah.

In 14 recorded Utah habitats it occurred 10 times in montane forest. In 10 elevational records between 4276 and 9000 ft, it occurred four times under 4900, three times between 7000 and 7900.

Camponotus modoc Wheeler

C. herculeanus var. *modoc* Wheeler, 1910, Ann. New York Acad. Sci. 20:299; Rees and Grundmann 1940:11; Cole 1942:388; Beck et al. 1967:68.

C. pennsylvanicus modoc: Ingham 1959:69.

Records (Map 3): **BOX ELDER**: Raft River Mts, Tacoma Mt (U), Wellsville Mts, Willard Basin (KU). **CACHE**: Green Cyn, Leeds Cyn (KU), Logan, Logan Cyn (C42). **CARBON**: Scofield 4 and 6 mi S (A). **DAGGETT**: Palisade Park (RG). **DUCHESNE**: Avintaquin Cmpgnd (A), Mirror Lake (BY), Trial Lake (U). **EMERY**: Ferron Res (RG). **GARFIELD**: Carcass Crk on Boulder Mt (U). **IRON**: Cedar Breaks Nat Mon (U), Cedar City (RAU). **KANE**: Long Valley Jct 11 mi W (159). **RICH**: Garden City, Monte Cristo (KU), Woodruff 18.4 mi W (A), Wyoming brdr 0.5 mi S on U16 (A). **SALT LAKE**: Big Cottonwood Cyn (C42), Brighton (U), Little Willow Cyn (C42), Red Butte Cyn, Salt Lake City (U), Taylorsville (C42). **SAN JUAN**: Monticello 5 mi W (U). **SANPETE**: Ephraim 8.8 mi E (A), Maple Cyn (U), Orangeville 23.9 mi W (A). **SUMMIT**: Kamas 21 mi E, Mirror Lake 6.4 mi N (A), Oakley (U). **TOOELE**: Deep Crk Mts (U). **UINTAH**: Dinosaur Nat Mon (GR63), Jct Red Cloud Loop rd and U44 14 mi W (A), E Wall Lake (in Uinta Mts) (U), Whiterocks Cyn (KU). **UTAH**: Provo, Santaquin 6.7 and 7.7 mi E, Silver Lake Flat, Tibble Fk Cyn (A), Utah Lake (U). **WASATCH**: Francis 8.1 mi E, Hanna 14.3 mi W, Soldier Summit 7.9 and 10.1 mi N (A), Strawberry Valley (C42). **WASHINGTON**: Kolob, Pine Valley (City) (159). **COUNTY UNKNOWN**: Woodburn (C42) (no such city listed in *Utah Gazetteer*).

Smith (1979:1426) lists this species as western United States, including Colorado, where it occurs in logs and stumps in forested areas. Gregg (1963:667) lists it in Colorado between 4800 and 11,300 ft under rocks and logs predominantly in conifer habitats. Hunt and Snelling (1975:22) list it from Arizona. La Rivers (1968:7) lists it from Nevada, where Wheeler and Wheeler (1978:392) found it between 6000 and 12,000 ft. They found it frequently in wood in North Dakota (1963). Cole (1942:388) indicates its habitat in Utah as logs and stumps of conifers at high elevations. Ingham (1959) found it in southern Utah in logs in sagebrush, fir, aspen, and ponderosa pine.

Seventy-two ants in 10 collections were found under logs. In 5 of these the ants were under the same log with ants of the genus *Formica*: once with *F. gnava*, once *F. podzolica*, once *F. gnava* and *F. neoclara*, once *F. fusca* and *F. subnuda*, and once *F. obscuriventris*, *F. podzolica*, and *F. subnitens*. Thirty-two ants in 2 collections were taken from inside a log, 15 ants in 2 collections from the base of a dead standing tree, one ant under a rock, one from a dead chipmunk, 12 in 4 collections crawling in the open, and 23 of 2 collections from ground burrows. The burrows did not have mounds: one of them was in an area of Oregon grape and herbs, where 13 ants were found, and the other, with 10 ants, was in sagebrush and grass. The burrows in the sage-grass habitat were also occupied by *F. neogagates*. Twelve collections were in aspen: 8 in association with conifers, one with grass, herbs, and shrubs, and one grass and herbs. Four collections were in conifers; one cottonwoods; one oak, grass, herbs, and sagebrush; one herbs and Oregon grape; and one grass and sagebrush. In 54 recorded Utah habitats it occurred 42 times in montane forest. In 23 elevations between 4200 and 10,399 ft, 11 collections were under 7000 and 12 over 8000.

These ants are awkward crawlers, and when they are disturbed they hide under debris. Beck et al. (1957:68) found it feeding on dead rodents in three instances in Utah.

Camponotus nearcticus Emery

C. marginatus var. *nearcticus* Emery, 1893, Zool Jahrb. Syst. 7:669.

C. caryae decipiens: Rees and Grundmann 1940:11.

C. nearcticus decipiens: Cole 1942:388.

C. nearcticus: Knowlton 1970:208, 1975:2.

Records (Map 2): **BOX ELDER**: Kelton Pass (K70), Wildcat Hills (KU). **CACHE**: Logan (KU). **SALT LAKE**: E Mill Crk Cyn (RG). **SUMMIT**: Mirror Lake 17.3 mi N (A). **TOOELE**: Tooele (US). **UINTAH**: Dinosaur Nat Mon (Gr63). **WASHINGTON**: St George (KU).

Smith (1979:1432) lists this as eastern to western United States, including Colorado and Idaho, where it lives in trees, logs, pine cones, and other wood products. Gregg (1963:675) lists it between 4800 and 7000 ft in duff and under logs predominantly in cottonwood-willow habitats in Colorado. Hunt and Snelling (1975:22) list it from Arizona. Wheeler and Wheeler (1963) found it frequently in wood in North Dakota. Cole (1942:388) indicates its habitat in Utah as standing dead trees.

One collection of 10 ants was taken from under a log in sagebrush, aspen, and conifers. In seven known specific habitats, it was taken twice in montane forest. Three known elevations are between 2760 and 4923 ft.

Camponotus novaeboracensis (Fitch)

Formica novaeboracensis Fitch, 1845, Trans. New York State Agr. Soc. 14:766.

C. herculeanus ligniperdus var. *noveboracensis*: Rees and Grundmann 1940:11; Cole 1942:388.

C. novaeboracensis: Smith 1979:1426.

Records (Map 3): **CARBON**: Myton rd 10.5 mi E US6 (A). **DAVIS**: Bountiful (U). **DUCHESNE**: Muellers Prk, Roosevelt (C42). **GARFIELD**: Carcass Crk (on Boulder Mt) (U). **GRAND**: Moab (U). **IRON**: Cedar City 7 mi E (A). **RICH**: Chalk Crk (U). **SALT LAKE**: Big Cottonwood Cyn, Butterfield Cyn, Ft Douglas, Emigration Cyn, Red Butte Cyn, Salt Lake City (U). **SAN JUAN**: La Sal (U). **TOOELE**: S Willow Cyn (U). **UTAH**: American Fk Cyn (U).

Smith (1979:1426) lists this species as eastern to western United States, including Utah and Colorado, nesting in logs and stumps in wooded areas. Gregg (1963:663) lists it from Colorado between 5500 and 8500 ft under logs predominantly in conifer forest. Wheeler and Wheeler (1963) found it frequently in wood in North Dakota.

One collection of four ants was from under a rock in pinyon and juniper, and the other of one ant under a log in mahogany. In 15 recorded Utah habitats it was taken 9 times in montane areas. In 10 known elevations between 4042 and 9000 ft it was found most frequently under 7000. In one collection, when the cover boulder was removed, the exposed ants crawled rapidly into a burrow.

Camponotus ocreatus Emery

C. maculatus ocreatus Emery, 1893, Zool. Jahrb. Syst. 7:673.

C. ocreatus: Ingham 1959:71.

Records: **DUCHESNE**: Duchesne 9 mi W (WU). **WASHINGTON**: Zion Nat Park (I59).

Smith (1979:1429) lists this species as southwestern United States, including Arizona and Nevada, nesting under stones. Cole (1966:20) found a nest under a stone in mixed shrubs in southern Nevada. Ingham (1959, 1963) found it in southern Utah under stones in sagebrush, juniper, galletagrass, rabbitbrush, winterfat, shadscale, greasewood, and alkali flats. In four recorded Utah elevations it was taken three times between 4000 and 5000 ft and once at 7000 in desert situations.

Camponotus rasilis Wheeler

C. fallax subsp. *rasilis* Wheeler, 1910, J. New York Ent. Soc. 18:227.

C. rasilis: Gregg 1963:677.

Record: **UINTAH**: Dinosaur Nat Mon (Gr63).

Gregg (1963:677) lists this species from Colorado between 4800 and 6970 ft in duff and decaying logs in pinyon-juniper-oak and cottonwood-willow habitats, and shows a Utah record. Hunt and Snelling (1975:22) list it from Arizona.

Camponotus sansabeanus (Buckley)

Formica San Sabeanus Buckley, 1866, Proc. Ent. Soc. Phila. 6:167.
C. maculatus sansabeanus: Rees and Grundmann 1940:11.
C. maculatus sansabeanus var. *torrefactus*: Rees and Grundmann 1940:11.
C. sansabeanus: Cole 1942:387.
C. sansabeanus torrefactus: Cole 1942:388; Creighton 1950:379; Grundmann 1958:165; Beck et al. 1967:68; Smith 1979:1429.
C. sansabeanus sansabeanus: Smith 1979:1429.

Records (Map 3): **GRAND**: Moab (G48). **IRON**: Parowan (RG). **SALT LAKE**: Big Cottonwood Cyn (U), Mill Crk Cyn, Salt Lake City (RG). **SUMMIT**: Mirror Lake 1 mi N (A). **UINTAH**: Dinosaur Nat Mon (Gr63). **UTAH**: Aspen Grove (BY). **COUNTY UNKNOWN**: Oris (RG) (? = Osiris in Garfield Co).

Smith (1979:1429) designated three subspecies, *bulimosus, sansabeanus,* and *torrefactus,* as primarily western United States, including Utah, Colorado, Arizona, and Nevada, nesting under stones. He designated the latter two subspecies as occurring in Utah. They may be separated by the scape of the major, which is lobulate at the base in *sansabeanus,* but not lobulate in *torrefactus.* Gregg (1963:669) lists this species from Colorado between 4500 and 7000 ft under rocks, under logs, and in large mounds in pinyon-juniper and cottonwood-willow habitats, and shows a Utah record. Cole (1942:387) indicates that in Utah it nests under stones in dry woods. Grundmann (1958:165) indicates that in Utah it may be found under stones in mountain brush-juniper areas.

One collection of 10 ants was under a log in conifers. In eight recorded Utah habitats four were in montane forest. In seven recorded elevations between 4042 and 10,050 ft three were under 5000. Beck et al. (1967:68) found it feeding on dead rodents in one instance in Utah.

Camponotus semitestaceus Emery

C. maculatus vicinus var. *semitestaceus* Emery, 1893, Zool. Jahrb. Syst. 7:668.
C. semitestaceus: Allred and Cole 1979:99.

Record (Map 2): **KANE**: Glen Cyn City (AC).

Smith (1979:1429) lists this species as mostly western United States, but no intermountain state is indicated. It nests under stones or in low crater mounds. Hunt and Snelling (1975:22) list it from Arizona. Allred and Cole (1979) found it in southern Utah in ephedra-grass and sagebrush. La Rivers (1968:7) lists it from Nevada. One record in Utah was taken at 3250 ft.

Camponotus vicinus Mayr

C. vicinus Mayr, 1870, Verh. Zool.-Bot. Ges. Wien 20:940; Grundmann 1958:165; Ingham 1959:71; Beck et al. 1967:68; Knowlton 1970:208, 1975:2; Allred and Cole 1979:97.
C. maculatus vicinus: Rees and Grundmann 1940:11.
C. sansabeanus vicinus: Cole 1942:387, 388; Hayward 1945:120.
C. sansabeanus vicinus var. *nitidiventris*: Cole 1942:387.
C. sansabeanus vicinus var. *luteangulus*: Cole 1942:388.

Records (Map 4): **BEAVER**: Minersville (US). **BOX ELDER**: Brigham, Brigham Cyn, Cedar Crk (City) (US), Dolphin Island (C42), Kelton, Kelton Pass, Locomotive Spngs (K70), Lucin (BAD), Mantua (US), Raft River Mts (BY), Snowville and 16 mi SW (KU), Willard (C42). **CACHE**: Cache Jct (C42), Green Cyn (KU), Logan, Logan Cyn, Providence Cyn, Trenton (C42). **CARBON**: Myton rd 10.5 mi E US6 (A). **DAGGETT**: Bridgeport (BAD) and 8 mi S (US), Browns Park (BY), Pipe Crk (US), Willow Crk (BY). **DAVIS**: Farmington (C42), Farmington Cyn (US). **DUCHESNE**: Myton (US), Roosevelt (C42), Sheep Crk (BY), Tabiona 11.6 mi E (A). **EMERY**: Ferron (RG). **GARFIELD**: Boulder Mt (G58), Bryce Cyn Nat Park (BY), Horse Valley (in Henry Mts) (U). **GRAND**: Dewey 3 mi N (U), Moab (RG) 14 mi N (U) and 15 mi SE (KU). **IRON**: Cedar City (RAU), Modena 10.4 mi NE (A), Parowan (C42), Shirts Cyn (RAU). **JUAB**: Callao (BAD), Diamond Cyn (C42), Lynndyl Sand Dunes (BY), Nephi 12.1 mi W, Ponderosa Cmpgnd (A), Tintic, Trout Crk (City) (C42). **KANE**: Glen Cyn City (AC), W Mt Carmel Jct (K59), Navajo Wells (BAD), Pink Coral Sand Dunes (US). **MILLARD**: Gandy (BAD), Swasey Spngs (RG), White Valley (C42). **MORGAN**: Morgan (US), Porterville, Sage Range Mts (KU). **PIUTE**: Fish Lake Jct 1 mi S (U), Marysvale (A). **RICH**: Sage Crk Jct 5.1 mi W (A). **SALT LAKE**: Big Cottonwood Cyn, Butterfield Cyn (C42), City Crk Cyn (U), Draper (US), Ft Douglas, Granite, E Mill Crk Cyn, Salt Lake City (C42). **SAN JUAN**: Abajo Mts (G58), Blanding (C42) and 8 mi N (U), Dead Horse Pt (BAD), Hole-in-the-Rock (U), La Sal Crk (RG), La Sal Jct (A), Mexican Water (BAD), Monticello 2 mi W (A) and 17 mi E (U), Nat Bridges Nat Mon (US), Navajo Mt (US), Pack Crk (US), Jct U95 and U261 7.7 mi W (A). **SANPETE**: Chester (C42), Ephraim (US), Ephraim Cyn (U), Mt Pleasant (BAD). **SEVIER**: Koosharem, Paradise Valley (BAD), Salina Cyn nr Fremont Jct (U). **TOOELE**: Benmore, Clover (C42), Dolomite (US), Gransville (C42) (? = Grantsville), Mercur (BAD), Orrs Ranch, Vernon (C42), S Willow Cyn (U), Willow Spngs (C42). **UINTAH**: Bonanza (US), Dinosaur Nat Mon (Gr63), Dry Fk rd 13.4 mi N U121 (A), Duchesne 9 mi W (WU) (? = Ft Duchesne), Pelican Lake (US). **UTAH**: American Fk (RG), Jordan Narrows, Mercur (US), Provo, Springville, Thistle (BY), Tibble Fk Cyn, Tibble Fk Lake 0.5 mi W (A). **WASATCH**: Deer Crk Res (U), Hanna 9.2 mi W, Midway 3.7 mi NW (A). **WASHINGTON**: Pine Valley (City), nr Short Crk (Arizona) (I59), Sunset Cyn (nr Virgin) (RAU), Zion Nat Park (BY). **WAYNE**: Fruita 5 mi SE (U), Torrey (BAD). **WEBER**: Ogden (C42).

Smith (1979:1430) lists this species from western United States, including Colorado, nesting under stones or rotting wood in soil. Gregg (1963:674) lists it between 3500 and 9600 ft. under rocks and logs in a variety of habitats in Colorado. Hunt and Snelling (1975:22) list it from Arizona. Cole (1966:20) found it in southern Nevada under rocks commonly in pinyon-juniper, also in open dry areas in Utah (1942:387). Wheeler and Wheeler (1978:393) found it between 6000 and 9100 ft in Nevada, and frequently under rocks in North Dakota (1963). It occurs in Utah under stones in juniper-brush habitats (Grundmann 1958:165). Ingham (1959, 1963) found it under rocks in pinyon-juniper, sagebrush, serviceberry, bur sage, rabbitbrush, galletagrass and greasewood in southern Utah. Allred and Cole (1979:97) found it in southern Utah in habitats of ephedra-vanclevea-grass, juniper-ephedra-grass, sagebrush, juniper-pinyon, grass-sagebrush, and mostly in blackbrush. They also found it in abundance in associations of sagebrush-grass, sagebrush-grass-rabbitbrush, and sagebrush-rabbitbrush and less abundant in a variety of other vegetative types in Idaho (Allred and Cole 1971:239).

There were 186 ants in 12 collections found under rocks, 3 in one collection singly in an open area, and 2 in one collection under a juniper log. In a juniper-sagebrush area in late June 12 miles west of Nephi in Juab County, 20 ants in one collection were found in a mound of *Pogonomyrmex occidentalis*, although no harvester ants were present. The carpenter ants had excavated a large chamber (or cleared out and enlarged the food cache area) about eight inches from the top of the mound. About 50 workers and 50 pupae were present. Eggs were found under one rock in late June. When the rock was removed, the ants attempted to carry the exposed eggs into the burrow.

Ten collections were in sagebrush: one in association with grass and herbs, one grass and juniper, one pinyon and juniper, one pinyon, one snowberry and oak, and one snowberry. One collection was in pinyon and juniper; one grass and oak; one oak; one grass, herbs, maple and oak; and two aspen and fir. In 124 recorded Utah habitats 35 were in montane forest. In 69 recorded elevations between 3250 and 9000 ft, 51 collections were between 4000 and 6000. Only one was under 4000, two over 8000. Beck et al. (1967:68) found it feeding on dead rodents in 13 instances in Utah.

Conomyrma bicolor (Wheeler)

Dorymyrmex pyramicus var. *bicolor* Wheeler, 1906, Bull. Amer. Mus. Nat. Hist. 22:342; Cole 1942:372; Grundmann 1958:164; Ingham 1959:64.
D. bicolor: Beck et al. 1967:69.
C. bicolor: Allred and Cole 1979:99; Smith 1979:1420.

Records (Map 5): **CACHE**: Hodges Cyn (KU). **EMERY**: Greenriver (U). **GRAND**: Dewey (U), Crescent Jct 5 and 18.8 mi S (A), Moab (C42). **IRON**: Cedar City 6.3 mi W (A), Columbia Iron Mines 7 mi W, Kanaraville (I59), Modena 5.3 mi W (A). **JUAB**: Callao (BAD), Provo 30 mi S (C42). **KANE**: Adairville (BAD), Kanab (C42), 5 mi E (A) and 5 mi N (I59). **MILLARD**: Desert Range Exp Sta (U). **SAN JUAN**: Blanding, Bluff, Glen Cyn Res, Hole-in-the-Rock (G58), La Sal Jct (A), Lost Eden, Mexican Hat (G58), Monticello (US), Nat Bridges Nat Mon (U), Rock Crk (G58). **UINTAH**: Bonanza 15 mi N, Jensen 7.5 mi E (A), Vernal (US). **WASHINGTON**: Grafton, Harrisburg Jct toward Hurricane, LaVerkin, Pintura, Rockville, Shivwits Indian Res, nr Shortcreek (Arizona), Snow Cyn, Springdale, Toquerville, Virgin City, Zion Nat Park (I59). **WAYNE**: Hanksville 17 mi S (US).

Smith (1979:1420) lists this species from southwestern United States, including Utah, Arizona, and Nevada, where it nests in irregular or craterlike mounds in exposed situations. Cole (1966:18) found it commonly in craterlike mounds in creosote bush habitats in southern Nevada. In Utah it inhabits lower elevations along canyon bottoms, where it builds craterlike mounds (Grundmann 1958:164). Ingham (1959, 1963) found it in southern Utah in flat or low crater mounds in creosote bush, sagebrush, pinyon-juniper, ponderosa pine, blackbrush, joshua trees, rabbitbrush, bur sage, sand sagebrush, four-wing saltbush, and shadscale. Allred and Cole (1979:99) found it in blackbrush in southern Utah.

There were 125 ants in four collections taken from small crater mounds less than one-half inch in height and about six inches in diameter, with the dorsal opening in the crater. One mound was at the edge of a clearing of an active colony of *Pogonomyrmex occidentalis*. One collection of 30 ants was taken from a burrow with no mound, in which winged forms were more abundant than the workers. Thirty ants in one collection were taken from a safari; the ants scurried out of line when disturbed. Twenty-two ants were taken in two collections crawling singly away from their burrows. These ants are fast runners. Occasionally many mounds may occur in close vicinity. Six collections were in grass: two in association with sagebrush, one old man sage, one greasewood, and one juniper. One collection was in sagebrush and matchbrush. Only once in 43 recorded Utah localities was it found in a montane area. It was taken between 2500 and 7066 ft at 35 known elevations, 24 of these between 4000 and 5000 ft. It was taken over 6000 ft only twice.

In one instance a nest of *Formica obtusopilosa*, around which *bicolor* workers were scurrying, was excavated five miles west of Modena in Iron County. When the eggs of the *Formica* were exposed, the *bicolor* ants ran into the excavated area and began carrying the eggs away. In the same area two harvester ants of *Pogonomyrmex occidentalis* were "tending" a *bicolor*, apparently dead, at the fringe of the harvester mound. Several *bicolor* ants kept darting at the harvester ants, not actually making contact, in what appeared to be a type of rescue effort. The harvesters demonstrated no apparent response to the aggressive *bicolor* ants. Beck et al. (1967:69) found it feeding on dead rodents in two instances in Utah.

Conomyrma insana (Buckley)

Formica insana Buckley, 1866, Proc. Ent. Soc. Phila. 6:165.

Dorymyrmex pyramicus: Rees and Grundmann 1940:6; Cole 1942:371; Creighton 1950:348; Ingham 1959:64; Beck et al. 1967:69.

D. pyramicus flavus: Cole 1942:371.

D. pyramicus pyramicus: Grundmann 1958:164.

C. insana: Allred and Cole 1979:97.

Records (Map 5): **BEAVER**: Frisco (BAD). **BOX ELDER**: Snowville (KU). **CACHE**: Leeds Cyn (KU). **CARBON**: Price 20 mi E (WU). **DAVIS**: Layton 1.5 mi S (A). **DUCHESNE**: Blue Bench (C42), Duchesne (BAD), Myton (US), Roosevelt (BAD). **EMERY**: Goblin Valley (BAD) and 10 mi E (KU), Greenriver (C42), Hanksville 16 mi N (KU), Hideout Cyn nr Green River (U), Huntington (BAD). **GARFIELD**: Escalante 20 mi E (U), Hite (BAD). **GRAND**: Arches Nat Park (WU), Dewey (U), Moab (C42). **IRON**: Cedar City (159), 3.7 mi E and 16.8 mi W (A), Little Pinto (US), Lund 19 mi N, Modena 10.4 mi NE (A), New Harmony 3 mi NW (159). **JUAB**: Nephi 5.5 mi W (A). **KANE**: Glen Cyn City (AC), Kanab (RG), Wahweap (KU). **MILLARD**: Desert Range Exp Sta (BAD), White Valley (C42). **PIUTE**: Kingston (BAD). **SALT LAKE**: Butterfield Cyn, Granite (C42), Mt Olympus (U), Parleys Cyn (C42), Riverton 2.6 mi S (A). **SAN JUAN**: Aztec Cyn (U), Blanding (G58), Bluff (KU) and 11 mi N (U), Hole-in-the-Rock Cyn (U), La Sal Jct 1.6 and 23.1 mi S (A), Monticello (G58), Nat Bridges Nat Mon (U), Squaw Flat Cmpgnd (in Canyonlands Nat Park) (WU), Jct U95 and U261 7.7 mi W, Jct U261 and US163 19.6 mi N (A). **SANPETE**: Yuba Res (BAD). **TOOELE**: Clive, Clover, Orrs Ranch, Tooele (C42). **UINTAH**: Bonanza (KU), Dinosaur Nat Mon (BAD), Ft Duchesne, Gusher (C42), Jensen (U) and 5.5 mi W (A), Lapoint, Ouray Valley (C42), Vernal 10 mi N (A). **UTAH**: Goshen, Lehi, Orem, Provo (C42). **WASHINGTON**: Central (159), Diamond Valley (BAD), Hurricane (C42), Leeds (US), Leeds Cyn (KU), Pine Valley Res (159), Rockville (BAD), Snow Cyn (KU), St George (C42), Toquerville (BAD), Virgin (KU), Zion Nat Park (WU). **WAYNE**: Capitol Reef Nat Park (WU), Fruita, Hanksville (BAD), and 17 mi S (KU), Loa (A), Torrey (BAD).

Smith (1979:1420) lists this species as eastern to western United States (no intermountain state listed), where it nests in irregular or craterlike mounds in open areas. Gregg (1963:434) lists it from Colorado between 3500 and 8500 ft under rocks in a variety of habitats, predominantly pinyon-juniper and grass. Hunt and Snelling (1975:22) list it from Arizona. Wheeler and Wheeler (1963) found it frequently in soil craters in North Dakota. Cole (1966:18) found it commonly in creosote bush habitats in southern Nevada. It forms craterlike nests in Utah (Cole 1942:371). Ingham (1959, 1963) found it in southern Utah in pinyon-juniper, sagebrush, creosote bush, mesquite, galletagrass, rabbitbrush, winterfat, shadscale, greasewood, and alkali flats. It was associated with *Solenopsis molesta* in one nest. Allred and Cole (1979:97) found it in a large variety of desert shrub associations in southern Utah, commonly in juniper-pinyon.

There were 178 ants of seven collections taken from small crater mounds. Two were in the cleared area of active colonies of *Pogonomyrmex occidentalis.* In Davis County 1.5 mi south of Layton on highway US89, many small craterlike mounds were in close vicinity and surrounding a mound occupied by *occidentalis.* Ten ants in one collection were taken from a mound actually on an occupied mound of *occidentalis.* Another mound occupied by *occidentalis* was covered with sticks, and many (30 collected) *insana* were crawling among the sticks. No openings or mounds for these small ants were seen, nor were any of their mounds in the vicinity of the harvester mound. No evidence was seen of the harvesters attacking the *insana,* and the two species seemingly intermingled in their movements over the large mound. Nineteen miles north of Lund on the road to Pine Valley in Iron County, nine occupied mounds were found on a large flattened mound of *occidentalis*. In San Juan County, 19.6 mi north of the junction of US163 and U261 along U261, *insana* had parts of three *occidentalis* with some appendages and parts of the body missing, as though chewed by the *insana*. Eighty ants in two collections were taken from safaris; in one case some of the ants were grouped around a dead moth. Forty-two ants in two collections were taken under rocks. In one of these colonies eggs were present in late June. Eight collections were in sagebrush: two in association with grass, one clover, one rabbitbrush, one juniper, one pinyon, and one juniper and pinyon. One collection was in grass and clover, one grass and herbs, one herbs, one matchbrush and greasewood, one rabbitbrush, and one juniper. In 87 recorded Utah localities it occurred only 5 times in montane areas. In 53 recorded elevations between 2750 and 7066 ft it was taken most frequently (32 times) between 4000 and 6000. Beck et al. (1967:69) found it feeding on dead rodents in 18 instances in Utah.

Crematogaster cerasi (Fitch)

Myrmica cerasi Fitch, 1855 (1854), Trans. New York State Agr. Soc. 14:835.

Record: **WASHINGTON**: Leeds (US).

Smith (1979:1378) lists this species as eastern to midwestern United States, no intermountain state listed, where it nests under rocks and logs. The one collection in Utah reportedly taken at 2750 ft is questionable.

Crematogaster coarctata Mayr

C. coarctata Mayr, 1870, Verh. Zool.-Bot. Ges. Wien 20:990.

C. vermiculata: Cole 1942:363.

Record: **JUAB**: Provo 30 mi S (C42).

Smith (1979:1378) lists this species as western United States, including Nevada, nesting under rocks. Cole (1966:16) found its nests in southern Nevada in open soil and under stones in pinyon-juniper and a variety of desert shrub types; it also occurs in sagebrush in Utah (Cole 1942:363). One Utah collection was taken at 4909 ft.

Crematogaster depilis Wheeler

C. lineolata opaca var. *depilis* Wheeler, 1908, Bull. Amer. Mus. Nat. Hist. 24:478.

C. depilis: Beck et al. 1967:68; Allred and Cole 1979:97.

Records (Map 6): **KANE**: Glen Cyn City (AC). **WASHINGTON**: Beaver Dam Wash, Toquerville (BAD).

Smith (1979:1378) lists this species as western United States, including Arizona and Nevada, nesting in roots and lower stems of desert plants. Cole (1966:16) found it in open areas in southern Nevada in various desert shrub types, none in pinyon-juniper. Allred and Cole (1979:97) found it in a variety of desert shrub habitats, most frequently in ephedra-vanclevea-grass and juniper-ephedra-grass associations in southern Utah.

In three desert collections in Utah it was taken betwen 2350 and 3371 ft. Beck et al. (1967:68) found it feeding on dead rodents in five instances in Utah.

Crematogaster emeryana Creighton

C. lineolata emeryana Creighton, 1950, Bull. Mus. Comp. Zool. 104:213; Grundmann 1958:163; Beck et al. 1967:68.

C. lineolata nr *cerasi*: Rees and Grundmann 1940:4; Cole 1942:363.

C. lineolata: Ingham 1959:55.

C. punctulata: Beck et al. 1967:69.

C. emeryana: Smith 1979:1378.

Records (Map 6): **BEAVER**: Minersville (BAD). **BOX ELDER**: Locomotive Spngs (BAD), Park Valley (City) (C42). **CACHE**: Logan (C42). **JUAB**: Callao (BAD). **KANE**: Mt. Carmel Jct (I59), Navajo Wells (BAD). **MILLARD**: Swasey Spngs (RG). **SALT LAKE**: Parleys Cyn (U). **SAN JUAN**: Blanding, Bluff, Monticello (G58), Montezuma Crk (BAD). **TOOELE**: Clover, Delle, Fisher Pass, Low (C42). **UTAH**: American Fk Cyn (U), Chimney Rock Pass (BAD), Provo (C42). **WASHINGTON**: Diamond Valley (BAD), Grafton, La Verkin, New Harmony, Pintura, Rockville, Santa Clara River, Zion Nat Park (I59). **WEBER**: Ogden Cyn (U).

Smith (1979:1378) lists this species as western United States, including Utah, Colorado, and Arizona, where it usually nests under rocks in mountains at elevations over 6000 ft. Gregg (1963) lists it between 3500 and 8000 ft in a variety of habitats, predominantly under rocks and logs in oak and pinyon-juniper areas in Colorado. Cole (1942:363) indicates its habitats in Utah as under stones, logs, and bark. Ingham (1959, 1963) found it under stones and wood in willow, poplar, tamarix, oak, juniper, ash, sagebrush, squawbrush, and shadscale in southern Utah.

In 29 localities, only three were in montane forest. In 25 known elevations between 3000 and 7066 ft, 10 were between 4000 and 5000. Beck et al. (1967:68) found it feeding on dead rodents in eight instances in Utah.

Crematogaster hespera Buren

C. hespera Buren, 1968, J. Georgia Ent. Soc. 3:98; Smith 1979:1379.

Record: **WASHINGTON**: Zion Nat Park (B).

Smith (1979:1379) lists this species as western United States, including Utah and Arizona, principally as an arboreal form in cottonwood trees. Buren (1968:100) indicates that it is largely an arboreal species of cottonwoods and other trees, but also occurs in logs at elevations between 2000 and 5500 ft. One Utah collection was taken at 4276 ft.

Crematogaster minutissima Emery

C. victima missouriensis Emery, 1895, Zool. Jahrb. Syst. 8:287.

C. minutissima: Beck et al. 1967:69.

Record: **WASHINGTON**: Diamond Valley (BAD).

Creighton (1950) and Smith (1979) list three subspecies as eastern to western United States, including Colorado and Arizona, nesting in soil at the base of stumps. The Utah form is likely *smithi*, although *missouriensis* may come into eastern Utah. The two may be separated by the smooth shining dorsum of the promesonotum in *smithi*, whereas in *missouriensis* it is finely punctate. Gregg (1963:364) lists this species at 4150 ft under rocks in grassy habitats in Colorado. Beck et al. (1967:69) found it feeding on dead rodents in one instance in Utah.

Crematogaster mormonum Emery

C. lineolata coarctata var. *mormonum* Emery, 1895, Zool. Jahrb. Syst. 8:284; Rees and Grundmann 1940:4.

C. coarctata var. *mormonum*: Cole 1942:363.

C. mormonum: Creighton 1950:215; Ingham 1959:56; Beck et al. 1967:69; Knowlton 1970:209; 1975:2; Allred and Cole 1979:99; Smith 1979:1380.

Records (Map 6): **BEAVER**: Frisco (BAD). **BOX ELDER**: Hansel Mts (K75), Snowville (KU) and 4 mi W (K70). **CACHE**: Leeds Cyn (KU). **JUAB**: Joy (BAD). **KANE**: Glen Cyn City (AC), Kanab (US). **MILLARD**: Swasey Spngs (BAD). **SALT LAKE**: E Mill Crk Cyn, Salt Lake City (RG). **SAN JUAN**: Bluff (KU). **SEVIER**: Koosharem (BAD). **TOOELE**: Stansbury Island (C42). **WASHINGTON**: Leeds (KU), Pine Valley Res (I59), Zion Nat Park (KU).

Smith (1979:1380) lists this species as western United States, including Utah, Nevada, and Idaho, nesting under rocks. Cole (1942:363) indicates its habitats in Utah as under stones and logs. Ingham (1959) found it under stones and logs in southern Utah. Allred and Cole (1979:99) found it in a saltbush-sagebrush association in southern Utah.

In 17 recorded Utah habitats it was taken only 3 times in montane forest. In 12 recorded elevations between 2750 and 6850 ft it was taken 6 times between 4000 and 5000, 4 times above 6000. Beck et al. (1967:69) found it feeding on dead rodents in four instances in Utah.

Crematogaster nocturna Buren

C. nocturna Buren, 1968; J. Georgia Ent. Soc. 3:112; Knowlton 1975:2; Smith 1979:1380.

Records: **BOX ELDER**: Hansel Mts (K75). **SAN JUAN**: Nat Bridges Nat Mon (B).

Smith (1979:1380) lists this species as western United States, including Utah and Arizona. In one Utah collection it was taken at 5700 ft.

Forelius foetidus (Buckley)

Formica foetida Buckley, 1866, Ent. Soc. Phila., Proc. 6:167.

Forelius foetida: Ingham 1959:64.

Records: **EMERY**: San Rafael Swell (U). **JUAB**: Chicken Crk Res (KU). **KANE**: Grosvenor Arch (US). **WASHINGTON**: Rockville (I59).

Smith (1979:1419) lists this species as midwest to western United States, including Colorado, nesting under various objects or in small craters. Gregg (1963:434) lists it between 4400 and 4900 ft under rocks in cottonwood-willow and grass habitats in Colorado. Hunt and Snelling (1975:22) list it from Arizona. LaRivers (1968:7) lists it from Nevada. Ingham (1959) found it in small crater mounds in sagebrush, blackbrush, cliffrose, Russian thistle, and cheatgrass in southern Utah. In four localities in Utah it was taken between 3800 and 5000 ft in desert areas.

Formica accreta Francoeur

F. accreta Francoeur, 1973, Soc. Ent. du Quebec, Mem. no. 3, pp 182–9.

Record: **WEBER**: Beaver Crk (KU).

Smith (1979:1452) lists this species from western United States, including Idaho.

Formica aerata Francoeur

F. aerata Francoeur, 1973, Soc. Ent. du Quebec, Mem. no. 3, pp. 116–22.

Record: **CACHE**: Tony Grove Lake (KU).

Smith (1979:1452) lists this species from western United States, including Nevada, nesting under rocks. In one Utah collection it was taken at 8075 ft.

Formica altipetens Wheeler

F. cinerea cinerea var. *altipetens* Wheeler, 1913, Bull. Mus. Comp. Zool. 53:399.

F. cinerea altipetens: Rees and Grundmann 1940:10; Cole 1942:383.

F. altipetens: Creighton 1950:531; Francoeur 1973:58; Smith 1979:1452.

Records (Map 7): **CACHE**: Ant Valley, Antelope Valley, Blacksmith Fk Cyn, Elk Valley, Franklin Basin, Logan Cyn, Petersboro, Pole Crk Spng, Rock Crk, Tony Grove (KU), Wellsville Cyn (F). **DUCHESNE**: Fruitland (U). **GARFIELD**: Boulder Mt (U). **GRAND**: Warner Ranger Sta (RG). **RICH**: Garden City (KU). **SAN JUAN**: Monticello (KU). **SUMMIT**: Henrys Fk Basin (RG). **TOOELE**: S Willow Cyn (U). **WASATCH**: Soldier Summit 1 mi E (A).

Smith (1979:1452) lists this species from western United States, including Utah, Colorado, Arizona, Idaho, and Wyoming, nesting in open areas sometimes with low mounds or under objects. Gregg (1963:507) lists it between 6000 and 11,000 ft under rocks and logs mostly in conifer areas in Colorado. La Rivers (1968:9) lists it from Nevada. Wheeler and Wheeler (1977) found it frequently in thatched or earthen mounds and under rocks in North Dakota. Cole (1942:383) indicates its habitats in Utah as under stones or in flat earthen mounds in open areas.

Four ants in one collection were found crawling singly on the ground in sagebrush and herbs. In 19 recorded Utah habitats 15 were in montane forest. In nine recorded elevations between 4471 and 10,500 ft it was found most frequently (four times) between 7000 and 9000.

Formica argentea Wheeler

F. fusca var. *argentata* Wheeler, 1902, Amer. Nat. 36:952; Cole 1942:383.

F. fusca argentea: Rees and Grundmann 1940:9; Knowlton 1970:209.

F. argentea: Francoeur 1973:150.

Records (Map 7): **BEAVER**: Beaver Crk (F). **BOX ELDER**: Cedar Hill, Clear Crk Cyn (KU), Kelton Pass (K70), Snowville (C42), Willard Basin (in Wellsville Mts) (KU). **CACHE**: Ant Valley, Bear River Mts (KU), Blacksmith Fk Cyn (C42), Elk Valley, Franklin Basin, High Crk, Leeds Cyn, Logan (KU), Logan Cyn (C42), Mendon (F), Paradise, Petersboro, Providence, Tony Grove Cyn, Tony Grove Lake (KU), Wellsville (F). **DAGGETT**: Sheep Crk (RG). **DAVIS**: Farmington, Farmington Cyn (KU). **EMERY**: Hideout Cyn nr Green River (U). **GARFIELD**: Orton (KU). **JUAB**: Ponderosa Cmpgnd, Red Crk Spng (KU). **KANE**: Mt Carmel (F), Wahweep (KU). **RICH**: Allen Cyn, Monte Cristo and 6 mi S, Randolph (WU). **SALT LAKE**: Garfield (F), Little Willow Cyn (C42). **SAN JUAN**: Monticello (RG) and 2 mi W (A). **SEVIER**: Burrville (U), Salina Cyn nr Fremont Jct (U). **TOOELE**: Delle (C42). **UINTAH**: Jct Dry Fk rd and Red Cloud Loop rd, Jct Red Cloud Loop rd and U44 9.2 mi W (A), Whiterocks (KU). **UTAH**: American Fk (RG), Spanish Fk Cyn (KU). **WASATCH**: Midway 3.7 mi NW, Strawberry Res 4 mi S (A). **WASHINGTON**: Pine Valley (City) (KU). **WAYNE**: Capitol Reef Nat Park (U). **WEBER**: head of Beaver Crk, Monte Cristo (KU). **COUNTY UNKNOWN**: Rand (F) (? = abbr for Randolph in Rich Co).

Smith (1979:1452) lists this species from eastern to western United States including Arizona, nesting in open or semiopen areas under rocks or in low mounds. Gregg (1963:523) lists it from Colorado between 4500 and 11,000 ft under rocks and wood in a variety of habitats. La Rivers (1968:9) lists it from Nevada, where Wheeler and Wheeler (1978:394) found it between 6200 and 11,500 ft. They also found it frequently under rocks, also in earthen mounds in North Dakota (1977). Cole (1942:383) indicates its habitats in Utah as under stones and logs in cold forests at higher elevations.

Twenty-four ants in four collections were taken from under rocks. In one collection it was under the same rock with *Formica lasioides*, once *F. fusca*, and once *F. pallidefulva* and *Pheidole desertorum*. Four specimens in one collection were taken singly crawling in the open. Two collections were in oak, one associated with grass. One collection was in legumes and sagebrush, one a grassy meadow, and one grass and sagebrush in an open area of aspen and pine. In 54 recorded Utah habitats it was taken 28 times in montane forest. In 23 recorded elevations between 4225 and 9300 ft it was taken 10 times under 5000, 12 times between 6000 and 9000.

Formica calviceps Cole

F. calviceps Cole, 1954, J. Tenn. Acad. Sci. 29:164.

Record: **UTAH**: Spanish Cyn (KU) (? = Spanish Fk Cyn).

Smith (1979:1457) lists this species only from New Mexico nesting under stones banked with detritus. Its occurrence in Utah is questionable.

Formica canadensis Santschi

F. cinerea var. *canadensis* Santschi, 1913, Ann. Soc. Ent. Belg. 57:435; Knowlton 1975:2.

F. cinerea: Rees and Grundmann 1940:10; Knowlton 1970:209.

F. cinerea neocinerea: Rees and Grundmann 1940:10; Cole 1942:383; Knowlton 1970:209, 1975:2.

F. cinerea lepida: Creighton 1950:531; Beck et al. 1967:69.

F. montana: Ingham 1959:82.

F. canadensis: Francoeur 1973:66; Smith 1979:1452.

F. cinerea canadensis: Knowlton 1975:2.

Records (Map 7): **BEAVER**: Puffers Woke (F) (? = Puffer Lake). **BOX ELDER**: Locomotive Spngs (K70), Park Valley (City) (KU), Snowville (C42), Wellsville Mts, Willard Basin (KU). **CACHE**: near Franklin (Idaho), Franklin Basin, Hyrum, Logan Cyn, Tony Grove Lake (KU), Wellsville (RG). **IRON**: Cedar Breaks Nat Mon, Cedar City (F), Newcastle (159). **KANE**: Kanab (C42), Navajo Lake (159). **RICH**: Laketown, Randolph (KU). **SALT LAKE**: Alta (U), Wasatch (RG). **SAN JUAN**: La Sal Mts (U), Montezuma Crk (BAD). **SANPETE**: Ephraim Cyn (KU). **SEVIER**: Venice (F). **SUMMIT**: Wasatch (RG). **TOOELE**: Clover (F). **UINTAH**: Bonanza (KU), Ft Duchesne (F), Jensen 17 mi SW (C42), Lapoint (F), Neola 2.7 mi E (A), Paradise Park (U), Vernal, Whiterocks (F). **UTAH**: Goshen (F), Lehi (BAD). **WEBER**: Beaver Crk (KU).

Smith (1979:1452) lists this species from midwest to western United States, including Utah, Colorado, Arizona, Idaho, and Wyoming, nesting in open or wooded areas in soil, sometimes with a low mound. Gregg (1963:511) lists it from Colorado between 3500 and 11,000 ft under rocks, wood, and in thatched hummocks predominantly in meadow situations. Allred and Cole (1971:239) found it rarely in associations of sagebrush-grass in Idaho. La Rivers (1968:9) lists it from Nevada. Wheeler and Wheeler (1977) found it frequently in earthen mounds, also commonly under rocks in North Dakota. Cole (1942:383) indicates its habitats as under stones or flat earthen mounds in open areas in Utah. Ingham (1959) found it in southern Utah under stones in sagebrush, aspen, fir, and spruce. Knowlton (1975:2) found it associated with rabbitbrush in northern Utah.

Forty ants in one collection were taken from the ground in grass near an irrigated field. In 38 recorded Utah habitats 13 were in montane forest. In 29 recorded elevations between 4495 and 10,399 ft, 18 were under 6000 and 7 were over 9000.

Formica ciliata Mayr

F. ciliata Mayr, 1886, Verh. Zool.-Bot. Ges. Wien 36:428; Rees and Grundmann 1940:9; Cole 1942:379; Creighton 1950:483; Grundmann 1958:165; Gregg 1963:546; Smith 1979:1457.

Records: **GRAND**: Warner Ranger Sta (Gr63). **SAN JUAN**: Blanding (RG), between Blanding and Vedura (C42) (? = Verdure). **SANPETE**: Wales 3.3 mi W (A).

Smith (1979:1457) lists this as a species of western United States, including Utah, Colorado, and Wyoming, with nests (sometimes thatched) in meadows or open woods. Gregg (1963:546) lists it between 5354 and 11,000 ft under rocks and logs principally in conifer habitats in Colorado, and lists a record for Utah. Wheeler and Wheeler (1963) found it only under rocks in North Dakota. Cole (1942:379) indicates its habitats as under stones or logs in Utah. Nests of this species are usually low, thatched mounds in meadows and open woods (Grundmann 1958:165). Seven ants in one collection in Utah were taken from under a rock in sagebrush and rabbitbrush near a meadow. One recorded elevation in Utah is 6103 ft.

Formica comata Wheeler

F. comata Wheeler, 1909, J. New York Ent. Soc. 17:85; Rees and Grundmann 1940:9; Cole 1942:379.

Records: **GARFIELD**: Carcass Crk (on Boulder Mt) (U). **SALT LAKE**: Mill Crk Cyn (RG). **SAN JUAN**: La Sal Mts (U).

Smith (1979:1457) lists this species as western United States, including Colorado, nesting under stones banked with thatch. Gregg (1963:550) lists it between 6000 and 7704 ft in sagebrush, chaparral, and grass habitats in Colorado. Cole (1942:379) indicates its habitats in Utah as under stones or logs, generally banked or covered with detritus. Two Utah collections were taken at 9000 ft.

Formica criniventris Wheeler

F. crinita Wheeler, 1909, J. New York Ent. Soc. 17:87.

F. crinoventris: Rees and Grundmann 1940:9.

F. criniventris: Cole 1942:379; Beck et al. 1967:69; Smith 1979:1457.

Records (Map 8): **BOX ELDER**: Garland (KU). **CACHE**: Blacksmith Fk Cyn (KU). **SALT LAKE**: Big Cottonwood Cyn, Brighton (U). **SEVIER**: Paradise Valley (BAD). **COUNTY UNKNOWN**: Boulton (RG) (? = Boulter in Juab Co).

Smith (1979:1457) lists this species as western United States, including Utah and Colorado, nesting under stones banked with thatch in meadows and open forests. Gregg (1963:550) lists it between 5100 and 5900 ft under rocks predominantly in gardens and open meadows in Colorado. Wheeler and Wheeler (1963) found it frequently under rocks in North Dakota. Cole (1942:379) indicates its habitat in Utah as under stones banded with detritus. Knowlton (1975:2) found it associated with rabbitbrush in northern Utah.

In six recorded Utah habitats it was taken four times in montane forest. Three known elevations are 4340, 5000, and 8600 ft. Beck et al. (1967:69) found it feeding on dead rodents in one instance in Utah.

Formica densiventris Viereck

F. fusca var. *densiventris* Viereck, 1903, Trans. Amer. Ent. Soc. 29:74.

F. rasilis spicata: Creighton 1950:507.

F. densiventris: Smith 1979:1462.

Records (Map 8): **BOX ELDER**: Snowville (KU). **CACHE**: Bear River Mts, Leeds Cyn (KU). **RICH**: Bear River, Wasatch Mts (KU).

Smith (1979:1462) lists this species from western United States, including Utah and Colorado, nesting in forests under stones and logs, occasionally thatched. Hunt and Snelling (1975:23) list it from Arizona. Wheeler and Wheeler (1978:394) found it between 7200 and 10,000 ft in Nevada. One collection in Utah was taken at 4544 ft.

Formica emeryi Wheeler

F. emeryi Wheeler, 1913, Bull. Mus. Comp. Zool. 53:389.

Record: **CACHE**: Cowley Cyn (KU).

Smith (1979:1464) lists this species only from Colorado, where it associates with *F. neogagates*. Gregg (1963:606) lists it at 6000 ft in meadow habitats in Colorado.

Formica fossaceps Buren

F. fossaceps Buren, 1942, Iowa State Coll. J. Sci. 16:402.

Record: **BOX ELDER**: Tremonton (KU).

Smith (1979:1458) lists this species from midwestern United States (no intermountain state listed), where it nests under stones or logs banked with thatch or in low earthen mounds covered with thatch or grass. Wheeler and Wheeler (1963) found it under rocks and in earthen mounds in North Dakota. One collection in Utah at 4315 ft is questionable.

Formica fusca Linnaeus

F. fusca Linnaeus, 1758, Syst. Nat. (10 ed.) 1:580; Cole 1942:381, 382; Creighton 1950:532; Grundmann 1958:165; Ingham 1959:81; Beck et al. 1967:69; Knowlton 1970:209, 1975:2.

F. fusca subaenescens: Rees and Grundmann 1940:9; Cole 1942:382.

F. fusca subsericea: Cole 1942:382.

F. marcida: Creighton 1950:534; Ingham 1959:82.

Records (Map 8): **BEAVER**: Beaver 5.5 mi E (U). **BOX ELDER**: Brigham (C42), Cedar Hill (K75), Clear Crk Cyn (KU), Hardup (K75), Kelton Pass (K70), Mantua, Portage (KU), Snowville (K70), Wellsville Mts (KU), Wildcat Hills (K75), Willard Basin (F). **CACHE**: Ant Valley, Antelope Valley, Bear River Mts, Beaver Crk, Blacksmith Fk Cyn, Elk Valley, Franklin Basin, Green Cyn, Hodges Cyn, Leeds Cyn, Logan (KU), Logan Cyn (C42), Mendon Cold Spngs, River Heights, Millville, Rock Crk, Tony Grove (KU). **EMERY**: Ferron (RG), Hideout Cyn nr Green River (U). **GARFIELD**: Boulder (U), Bryce Cyn Nat Park (WU), Carcass Crk (on Boulder Mt) (U). **IRON**: Cedar Breaks Nat Mon (F), Cedar City 19 mi E (A). **JUAB**: Indian Farm Cyn (U). **KANE**: Cedar City 24.3 mi E (A), Glendale (159), Kanab Cyn (C42). **RICH**: Garden City, Meadowville and 8 mi NW, Monte Cristo (KU). **SALT LAKE**: Big Cottonwood Cyn, Brighton, Butterfield Cyn, Mt Olympus, Red Butte Cyn (U), Salt Lake City (C42). **SAN JUAN**: Abajo Mts (G58), La Sal Crk (RG), Monticello (U). **SANPETE**: Bluebell Flats (KU), Ephraim Cyn (U), Pleasant Crk (BAD). **SUMMIT**: Kamas 21 mi E, Mirror Lake 1 and 6.4 mi N (A), Soapstone Ranger Sta (U), Wyoming brdr on U150 (A). **TOOELE**: Clover, Fisher Pass, Grantsville, Tooele (C42), S Willow Cyn (U). **UINTAH**: Ashley Crk nr Vernal (U), Dry Fk rd 15 and 22.8 mi N U121 (A). **UTAH**: American Fk Cyn (U), Aspen Grove (BY), Halls Fk rd 5.2 mi N from Hobble Crk rd (A), Provo (BY), Silver Lake Flat (A). **WASATCH**: Francis 8.1 mi E (A), Heber (U). **WASHINGTON**: Kolob (159), Pine Valley (City) (BAD). **WEBER**: Beaver Crk, Lime Spngs, Monte Cristo 6 mi S (KU), Ogden (C42). **COUNTY UNKNOWN**: Current Crk (C42) (? = Currant Crk either in Duchesne, Utah, or Wasatch Co).

Smith (1979:1452) lists this as an eastern to western species including Arizona, which nests in a variety of situations in soil and under rocks and logs in forests or open areas. Gregg (1963:517) lists it from Colorado between 5154 and 12,500 ft under rocks and logs and in thatched domes in a variety of habitats, predominantly in conifers, oak, and pinyon-juniper. Wheeler and Wheeler (1978:395) found it between 6100 and 11,500 ft in Nevada, and nesting frequently in wood in North Dakota (1977). Allred and Cole

(1971:239) found it in Idaho in an association of juniper-rabbitbrush-winterfat-sagebrush-grass. Grundmann (1958:165) designated it as a stream-side species in Utah between 4500 and 10,000 ft under stones or in low irregular mounds with numerous openings. Ingham (1959) found it under stones and logs in aspen, fir, spruce, and bristlecone pine in southern Utah. Cole (1966:23) found it in southern Nevada under stones restricted to pinyon-juniper, under stones and logs, and sometimes in craters or small earthen mounds at rather high elevations in Utah (1942:381). Knowlton (1975:2) found it associated with grass, sagebrush, shadscale, and rabbitbrush in northern Utah.

There were 122 ants in eight collections taken from under rocks. In one collection it was under the same rock with *Formica argentea*, once *F. gnava*, once *F. podzolica*, once *F. podzolica* and *Solenopsis molesta*, and once *F. gnava*, *Myrmica emeryana*, and *M. monticola*. In the association with *gnava* and *Myrmica*, when the rock was removed and the ants disturbed, some began pulling on the legs of others. In the association with *podzolica* and *Solenopsis*, the earth under the huge rock was divided into separate conspicuous dwelling levels in which the *Formica* occurred. The smaller *Solenopsis* were in a separate burrow. Thirty-eight ants in one collection were in a burrow with *Polygerus breviceps* under a log. Forty-one ants in three collections were found under logs, once under the same log with *Formica gnava* and *F. podzolica*, and once with *F. subnuda* and *Lasius alienus*. One ant was found in the open crawling on the ground. Six collections were in aspen: two in association with grass, sagebrush, and pine; one grass, herbs, and pine; and one pine. Three collections were in conifers; two in a grass, sedge, and herb meadow; one sagebrush; and one cottonwoods. In 82 recorded Utah habitats 49 were in montane areas. In 45 known elevations between 4288 and 10,500 ft, 20 were under 6000 and 3 were over 10,000. Beck et al. (1967:69) found it feeding on dead rodents in two instances in Utah.

Formica gnava Buckley

F. gnava Buckley, 1866, Proc. Ent. Soc. Phila. 6:156; Smith 1979:1453.

F. foreliana: Rees and Grundmann 1940:9; Cole 1942:380.

F. rufibarbis gnava: Rees and Grundmann 1940:10; Cole 1942:383; Creighton 1950:539; Ingham 1959:82; Allred and Cole 1979:98.

Records (Map 8): **DUCHESNE**: Avintaquin Cmpgnd (A). **GARFIELD**: Boulder Mt (U). **GRAND**: Dewey (U). **IRON**: Cedar City 19 mi E (A). **KANE**: Glen Cyn City (AC). **MORGAN**: Morgan (C42). **PIUTE**: Marysvale 4.1 mi S (A). **RICH**: Woodruff 18.4 mi W (A). **SALT LAKE**: Big Cottonwood Cyn (U). **SAN JUAN**: Rainbow Bridge Nat Mon (F). **SANPETE**: Orangeville 23.9 mi W, Skyline Drive 1 mi N Jct Orangeville and Ephraim rds (A). **SUMMIT**: Kamas 26.4 and 28.5 mi E, Mirror Lake 1 and 17.3 mi N (A), Park City (F). **UINTAH**: Red Cloud Loop rd 14 mi W U44 (A). **UTAH**: Halls Fk rd 5.2 mi N Hobble Crk rd (A), Lehi (RG), Nebo Loop rd 0.8 mi S Santaquin Cyn, Payson Cyn 12.3 mi up, Santaquin 6.7 mi E (A). **WASATCH**: Hanna 14.3 mi W (A). **WASHINGTON**: Snow Cyn (I59). **WEBER**: Ogden Cyn (C42).

Smith (1979:1453) lists this species from western United States, including Utah, Colorado, Arizona, and Nevada, nesting under rocks in desert areas or open woods. Gregg (1963:539) lists it between 5333 and 9000 ft under rocks and in thatched nests predominantly in pinyon-juniper-oak habitats in Colorado. Cole (1942) indicates its habitat in Utah as under stones or nests without craters in open areas. Ingham (1959, 1963) found it in soil-lacking mounds in sand sage in southern Utah. Allred and Cole (1979:98) found it in juniper-ephedra-grass and ephedra-grass habitats in southern Utah.

There were 281 ants in 11 collections taken from under logs. In one collection it was under the same log as *Formica fusca* and *F. podzolica*, once with *F. subnuda*, once *F. neoclara* and *Camponotus modoc*, once *C. modoc*, and once *Myrmica brevispinosa*. Ninety ants in 2 collections were taken from inside a log. There were 131 ants in 7 collections taken from under rocks. In one collection *gnava* was under the same rock as *F. fusca*; once with *fusca*, *Myrmica emeryana*, and *M. monticola*; once *F. podzolica*; and once *F. neogagates*, *F. obtusopilosa*, and *F. perpilosa*. When the rock covering *gnava* and *fusca* was removed, some ants were seen pulling others by their legs. The ants being pulled seemed not to demonstrate a defensive or aggressive behavior to the "pullers," suggesting a captive arrangement rather than fighting between different colonies. Ten ants in one collection were found under a slab of bark on the ground, and one ant was taken in the open. Immatures were found under one rock. Eleven collections were in aspen: 4 in association with fir, 3 with other conifers, one sagebrush and conifers, and one grass, herbs, and fir. Six collections were in conifers, 4 grass-herb meadows, and one sagebrush. In 26 recorded Utah habitats it was taken 18 times in montane forest. In 10 known elevations between 2900 and 10,500 it was taken 6 times under 5000, once over 7000 ft.

Formica haemorrhoidalis Emery

F. rufa integra var. *haemorrhoidalis* Emery, 1893, Arb. Zool. Jahrb. Syst. 7:644.

F. truncicola integroides var. *haemorrhoidalis*: Rees and Grundmann 1940:8.

F. rufa haemorrhoidalis: Cole 1942:381.

F. integra haemorrhoidalis: Creighton 1950:488; Beck et al. 1967:70.

F. haemorrhoidalis: Knowlton 1970:209, 1975:3.

Records (Map 9): **BOX ELDER**: Hansel (KU), Kelton (K70) and 9 mi N (KU), Snowville (K75), Trematon (KU) (? = Tremonton). **CACHE**: Avon, Bear River Mts, Green Cyn, Elk Valley, Leeds Cyn (KU), Hyde Park (C42), Logan Cyn, Smithfield Cyn (KU). **CARBON**: Myton rd 15 mi E US6 (A), Scofield (BAD). **DAGGETT**: Deep Crk (BAD). **DAVIS**: Kaysville (C42). **DUCHESNE**: Duchesne 12.4 mi S (A). **GARFIELD**: Bryce Cyn Nat Park (RG). **JUAB**: Callao 5 mi E(A). **RICH**: Chalk Crk (U). **SAN JUAN**: Blanding, Monticello (U). **SUMMIT**: Kamas 9.2 mi E (A). **TOOELE**: Mercur (BAD). **UTAH**: Eureka 0.5 mi E (A), Spanish Fk Cyn (KU). **WASATCH**: Midway 3.7 mi NW (A).

Smith (1979:1458) lists this species from midwest to western United States, including Colorado, nesting under logs or stones in areas of moderate to sparse cover. Gregg (1963:556) lists it between 5100 and 10,000 ft under rocks and logs in thatched nests predominantly in conifer habitats in Colorado. Allred and Cole (1971:239) found it in Idaho abundantly in an association of wild ryegrass, moderately so in rabbitbrush-sagebrush-grass, and rarely in rabbitbrush-sagebrush-grass-winterfat. La Rivers (1968:9) lists it from Nevada. Wheeler and Wheeler (1977) found it frequently in thatched mounds in North Dakota. Nests in Utah are under logs or stones, usually with a scattering of detritus on the periphery (Cole 1942:381). Knowlton (1975:3) found it associated with sagebrush in northern Utah.

Thirty-two ants in three collections were found under rocks. Once it was under the same rock as *Formica integroides*, and once with *Solenopsis molesta*. In the latter case the burrows of the two species were separate. Forty ants were taken from a mound of soil covered with a layer of sticks. Three ants in two collections were taken in the open. When disturbed in their colony these ants frequently rear back on their 2nd and 3rd legs, tucking the abdomen underneath, leaving the front legs and mandibles in an upward, apparently defensive position. Four collections were in sagebrush: one in association with herbs; one grass and herbs; one grass, herbs, serviceberry, cliffrose, juniper, and pinyon; and one aspen and conifers. One collection was in greasewood, and one in oak. In 28 recorded Utah habitats it was taken 13 times in montane forest. In eight known elevations between 4225 and 7977 ft it was found most frequently below 5000 and above 6000. Beck et al. (1967:70) found it feeding on dead rodents in four instances in Utah.

Formica hewitti Wheeler

F. hewitti Wheeler, 1917, Proc. Amer. Acad. Arts Sci. 52:552; Creighton 1950:533; Smith 1979:1453.

Records: **BOX ELDER**: Locomotive Spngs (KU). **CACHE**: W Hodges Cyn (KU). **GRAND**: Warner Ranger Sta (F).

Smith (1979:1453) lists this species from eastern to western United States, including Utah, nesting under rocks or wood in woods and forests. Gregg (1963:526) lists it from Colorado between 5354 and 10,000 ft under rocks and logs predominantly in conifer habitats. Wheeler and Wheeler (1978:395) found it between 6700 and 11,600 ft in Nevada. Allred and Cole (1971:239) found it in Idaho in an association of rabbitbrush-sagebrush-grass-winterfat. One collection in Utah was at 9750 ft.

Formica integroides Emery

F. rufa obscuriventris var. *integroides* Emery, 1893, Zool. Jahrb. Syst. 7:644.

F. truncicola integroides: Rees and Grundmann 1940:8.

F. trunciola integroides var. *coloradensis*: Rees and Grundmann 1940:8.

F. integroides: Rees and Grundmann 1940:8.

F. rufa coloradensis: Cole 1942:381.

F. integroides coloradensis: Creighton 1950:489; Ingham 1959:79; Smith 1979:1458.

F. integroides planipilis: Knowlton 1970:209, 1975:5.

F. integroides propinqua: Smith 1979:1459.

Records (Map 9): **BOX ELDER**: Hansel Mts, Locomotive Spngs, Snowville, Wellsville Mts, Willard Basin

(KU). **CACHE**: Bear River Mts, Blacksmith Fk Cyn, Franklin Basin, Leeds Cyn (KU), Logan Cyn (RG), Mendon Cold Spng, Monte Cristo (KU), Providence (C42), Tony Grove Cyn, W Hodges Cyn (KU). **CARBON**: Myton rd 15 mi E US6 (A). **GRAND**: Warner Ranger Sta (Gr63). **JUAB**: Eureka 0.5 mi E (A), McClellan Lake, NE Nephi (KU). **KANE**: Duck Crk Ranger Sta (C42). **MILLARD**: Swasey Spngs (RG). **RICH**: Randolph, Sage Crk (KU), Utah-Wyoming brdr 0.5 mi S on U16 (A). **SALT LAKE**: Big Cottonwood Cyn (U). **SANPETE**: Wales 3.3 mi W (A). **UINTAH**: Dry Fk rd 22.8 mi N U121 (A), Paradise Park 11 mi S (U). **UTAH**: Thistle 14.6 and 20.4 mi E, Tibble Fk Cyn (A). **WASATCH**: Daniels Cyn (RG). **WASHINGTON**: Kolob (I59). **WEBER**: Hooper, Slaterville (C42).

Creighton (1950) lists six and Smith (1979:1458) five subspecies from western United States, including Utah, Colorado, Nevada, and Idaho, nesting under logs that are usually thatched. The four that have been recorded from Utah may be separated by the following key.

1.	Erect hairs other than double row on middle and hind tibiae abundant	2
—	Erect hairs consist only of a double row on flexor surface	3
2(1).	Head and thorax clear red, legs about same color as thorax	*coloradensis*
—	Head and thorax of smaller workers marked with brown, legs brownish black	*planipilis*
3(1).	Occipital angles of head with erect hairs	*integroides*
—	Occipital angles of head lack erect hairs	*propinqua*

Gregg (1963) lists this species between 5354 and 12,000 ft under rocks, logs, and in thatched nests predominantly in conifer habitats in Colorado, and lists a record for Utah. Cole (1966:23) found it in southern Nevada only in pinyon-juniper, nesting in thatched mounds adjacent to shrubs. It also nests under logs with an adjacent thatching of detritus, resulting in dome-shaped mounds in Utah (Cole 1942:381). Wheeler and Wheeler (1978:394) found it between 5600 and 10,200 ft in Nevada. Ingham (1959) found it in mounds of detritus in sagebrush and oak in southern Utah. Knowlton (1975:5) found it in thatched nests in northern Utah.

Fifty ants in four collections were taken from mounds of sticks, one of them mixed with soil next to a log. In this latter case, ants of *Formica obscuripes* and *F. obscuriventris* were also present. In two other mounds ants of *F. oreas* were present. Ninety ants in three collections were taken from under rocks, once under the same rock with *F. laeviceps* and once with *F. haemorrhoidalis*. Four ants in one collection were found crawling in the open. Immature stages were found under two rocks in late June and early July. Six collections were in sagebrush: one in association with grass; one grass and herbs; one grass, herbs, and rabbitbrush; one grass, clover, and Russian thistle; one grass, shrubs, juniper, and pinyon; and one herbs, rabbitbrush, maple, and oak. One collection was in aspen. In 35 recorded Utah habitats it was taken 19 times in montane areas. In 14 known elevations between 4240 and 8555 ft it was collected most frequently under 5000 and over 8000.

Formica laeviceps Creighton

F. rufa laeviceps Creighton, 1940, Amer. Mus. Nat. Hist. Nov. 1055:7; Cole 1942:380.

F. laeviceps: Creighton 1950:491; Smith 1979:1459.

Records (Map 9): **BOX ELDER**: Snowville (US). **CACHE**: Hyde Park (KU). **DAVIS**: Kaysville (US). **GRAND**: Warner Ranger Sta (C42). **JUAB**: Nebo Loop rd 9.9 mi S Santaquin Cyn (A). **SALT LAKE**: Big Cottonwood Cyn, Mt Dell Res (U). **SANPETE**: Wales 3.3 mi W (A). **SUMMIT**: Chalk Crk (U). **TOOELE**: Tooele Cyn (U). **WASHINGTON**: Pine Valley (City) (US). **WEBER**: Slaterville (US).

Smith (1979:1459) lists this species from midwest and western United States, including Utah and Colorado, nesting under stones and logs with little debris in open areas. Gregg (1963:564) lists it between 5200 and 8500 ft in sagebrush and grass habitats in Colorado. Cole (1942:380) indicates that it nests under stones and logs in areas of moderate to sparse cover in Utah.

Ten ants in one collection were taken from under a rock in association with *Formica integroides*. Twenty ants in two collections were taken crawling on the ground in open areas. Three collections were in sagebrush, two in association with rabbitbrush. In 12 recorded Utah habitats it was taken 7 times in montane forest. In 8 recorded elevations between 4240 and 9750 ft it was taken most frequently under 5000, once over 8000.

Formica lasioides Emery

F. lasioides Emery, 1893, Zool. Jahrb. Syst. 7:646.
F. neogagates lasioides var. *vetula*: Rees and Grundmann 1940:10; Cole 1942:384.

Records (Map 9): **BOX ELDER**: Wellsville Mts (KU). **CACHE**: Ant Valley, Antelope Valley, Beaver Mt, Blacksmith Fk Cyn, Elk Basin, Franklin Basin, Green Cyn, W Hodges Cyn, Hyrum, Leeds Cyn, Logan Cyn, Millville, Monte Cristo, Pole Crk Spng, Ricks Spng, Tony Grove (KU). **EMERY**: Ferron Res, Green River, Gunnison Butte (RG). **GRAND**: Warner Ranger Sta (C42). **JUAB**: Deep Crk Mts (U). **RICH**: Garden City (KU), Randolph, and 8 and 10 mi S, Sage Crk (KU). **SALT LAKE**: Big Cottonwood Cyn (U). **SANPETE**: Ephraim Cyn, Majors Flats (KU). **SUMMIT**: Mirror Lake 11.6 mi N (A). **UINTAH**: Bonanza, Elk Basin, Hyrum, Millville (KU). **UTAH**: Nibley (KU), Payson Cyn 7.3 mi up (A). **WASATCH**: Strawberry Res 4 mi S (A). **WASHINGTON**: Pine Valley Cmpgnd (KU). **WEBER**: Beaver Crk (KU), Wolf Crk (U). **COUNTY UNKNOWN**: Beaver Head (KU).

Smith (1979:1449) lists this species from midwest to western United States, including Colorado and Arizona, nesting under stones or in soil or small craters. Gregg (1963:500) lists it between 4800 and 10,505 ft under rocks and wood in a variety of habitats in Colorado. Cole (1966:23) found its nests in southern Nevada under stones in pinyon-juniper, and indicated that some ants construct small craters in Utah (1942:384). Wheeler and Wheeler (1978:393) found it between 6200 and 10,900 ft in Nevada, and frequently under rocks in North Dakota (1963). Allred and Cole (1971:239) found it in Idaho in associations of wild rye-grass and rabbitbrush-sagebrush.

Twenty ants in two collections were taken from under rocks, once under the same rock with *Formica argentea* and once with *F. obscuriventris*. Four ants in one collection were taken singly in the open. Three collections were in sagebrush: one in association with legumes and two with aspen and conifers. In 39 recorded Utah habitats it was taken 26 times in montane forest. In 13 known elevations between 4087 and 11,000 ft it was taken most frequently under 6000, once over 10,000.

Formica limata Wheeler

F. limata Wheeler, 1913, Bull. Mus. Comp. Zool. 53:400; Creighton 1950:458; Beck et al. 1967:70; Smith 1979:1450.

Records (Map 10): **BOX ELDER**: Raft River Mts (U). **KANE**: Adairville (BAD). **SAN JUAN**: Pack Crk (KU). **SEVIER**: Fremont 9.7 mi N (A), Koosharem (BAD), Richfield 2.3 mi S (A). **TOOELE**: Dugway 11.9 mi E (A). **WASATCH**: Francis 8.1 mi E (A). **WEBER**: Woodruff 34.8 mi W (A).

Smith (1979:1450) lists this species from midwest and western United States, including Utah, Colorado, and Nevada, nesting under stones or in craters in grasslands. Gregg (1963:502) lists it between 5000 and 9700 ft under rocks and logs in a variety of habitats in Colorado. Wheeler and Wheeler (1963) found it frequently under rocks in North Dakota. Cole (1966:24) found its nests under stones in pinyon-juniper in southern Nevada.

Sixty ants in three collections were taken from under rocks. In one case they were under the same rock with *Formica neoclara*, once *F. occulta*, and once *F. podzolica*. Nine ants in two collections were taken in the open on the ground. Immatures were found under one rock in early August. Two collections were in sagebrush, one associated with matchbrush. One collection was in Russian thistle, one cottonwoods, and one juniper and pinyon. In nine recorded Utah habitats it was found four times in montane forest. In three collections it was taken at 5350, 5375, and 6850 ft. Beck et al. (1967:70) found it feeding on dead rodents in two instances in Utah.

Formica manni Wheeler

F. manni Wheeler, 1913, Bull. Mus. Comp. Zool. 53:389; Rees and Grundmann 1940:8; Cole 1942:378; Ingham 1959:77; Knowlton 1970:209; 1975:3; Smith 1979:1450.

Records (Map 10): **BOX ELDER**: Cedar Hill (US), Curlew Jct (K70), Hansel Mts (K75), Hardup (C42), Kelton (K75), 5 mi N (US) and 9 mi NW (KU), Kelton Pass (K70), Lampe (C42) (? = Lampo), Locomotive Spngs (K75), Promontory (KU), Snowville (K70), 6 mi W (KU) and 17 mi SW (KU), Wildcat Hills (US), Willard (C42). **CACHE**: Green Cyn (KU), Logan (C42). **MILLARD**: Tule Spngs (C42). **RICH**: Allen Cyn (KU). **SALT LAKE**: Wasatch Mts (RG). **TOOELE**: Stansbury Island (C42). **UTAH**: Jordan Narrows (C42), Silver Lake Flat (A). **WASATCH**: Kamas 11 mi SE (U). **WASHINGTON**: Leeds (RG), St George (KU).

Smith (1979:1450) lists this species from western United States, including Utah, Nevada, and Idaho, nesting under stones in desert areas. Allred and Cole (1971:239) found it in Idaho in an association of sagebrush-grass, rarely in other shrub types. Cole (1942:379) indicates its habitat as under stones in Utah. Ingham (1963) found it in juniper, sagebrush, galletagrass, rabbitbrush, winterfat, shadscale, and greasewood in southern Utah. Knowlton (1975:3) found it associated with rabbitbrush in northern Utah.

One specimen was taken from under a log in grass of an open area of aspen. Twenty-one ants of *Formica subnuda* were under the same log. In 27 recorded Utah habitats it was taken five times in montane areas. In 13 known elevations between 2750 and 9000 ft it was taken most frequently between 4000 and 5000, twice over 5000.

Formica microgyna Wheeler

F. microgyna Wheeler, 1903, Bull. Amer. Mus. Nat. Hist. 19:645; Creighton 1950:504; Gregg 1963:586; Knowlton 1975:3; Smith 1979:1462.

Records: **BOX ELDER**: Hansel Mts (KU), Snowville (K75). **CACHE**: Leeds Cyn (KU). **GRAND**: Warner Ranger Sta (Gr63).

Smith (1979:1462) lists this species from western United States, including Utah, Colorado, Nevada, and Wyoming, nesting under thatched stones in meadows and open forest. It is frequently associated with *Formica argentea*, *F. lasioides*, and *F. neogagates*. Gregg (1963:586) lists it between 5800 and 9400 ft under rocks and logs and in thatched nests predominantly in conifer habitats in Colorado, and gives a record for Utah. Cole (1966:24) found one worker in pinyon-juniper in southern Nevada. One collection in Utah was taken at 4544 ft.

Formica mucescens Wheeler

F. truncicola mucescens Wheeler, 1913, Bull. Mus. Comp. Zool. 53:392; Creighton 1950:491.

F. rufa mucescens: Cole 1942:380.

F. mucescens: Smith 1979:1460.

Records: **GARFIELD**: Bryce Cyn Nat Park (C42). **SANPETE**: Wales 3.3 mi W (A).

Smith (1979:1460) lists this species from Utah and Colorado nesting under stones in open areas. Gregg (1963:566) lists it between 5500 and 8750 ft under rocks and in thatched nests in grass in conifer habitats in Colorado. Cole (1942:380) indicates its habitats in Utah as under stones and logs.

Four ants in one collection were taken under a rock in an association of sagebrush, rabbitbrush, maple, and oak. In one collection it was taken at 7977 ft.

Formica neoclara Emery

F. fusca var. *neoclara* Emery, 1893, Arb. Zool. Jahrb. Syst. 7:646; Cole 1942:383.

F. neoclara: Creighton 1950:535; Beck et al. 1967:70; Knowlton 1970:209, 1975:3; Francoeur 1973:92.

F. pruinosa: Beck et al. 1967:70; Knowlton 1970:210, 1975:4.

Records (Map 10): **BEAVER**: Beaver (U), Beaver Cyn (F). **BOX ELDER**: Bear River City, Brigham, Corinne, Garland (US), Hansel Mts (US), Hardup, Kelton (K70) and 6 mi N (KU), Lucin (BAD), Mantua (F), Morton Cold Spngs (KU), Newton (F), Riverside (US), Snowville (K70), Tremonton (F), Willard (US), Willard Basin (KU). **CACHE**: Amalga (US), Ant Valley, Blacksmith Fk Cyn, Carter Crk, Clarkston, Franklin Basin, W Hodges Cyn (KU), Hyde Park (F), Lewiston, Logan (C42), Logan Cyn (KU), Mendon, Millville, Monte Cristo, Newton (KU), Paradise (US), Providence (KU), Smithfield (C42), Smithfield Cyn, Tony Grove (KU), Trenton (F), Wellsville (C42). **CARBON**: Clear Crk Cyn, Price (F) and 2 mi S (U). **DAVIS**: Farmington (F), Kaysville (US), Layton (F). **DUCHESNE**: Lake Atwood, Roberts Pass (BY). **EMERY**: Hideout Cyn nr Green River (U), Huntington (KU). **IRON**: Paragonah (U). **JUAB**: Topaz Mt (KU). **KANE**: Alton, Orderville (F). **MORGAN**: Morgan (BAD), Porterville (KU). **RICH**: Allen Cyn (KU), Chalk Crk (U), Laketown, Monte Cristo (KU). **SALT LAKE**: Brighton (C42), Hunter, Murray (US), Salt Lake City (C42). **SANPETE**: Orangeville 23.9 mi W (A), Palisade (KU). **SEVIER**: Aurora (F), Richfield 2.3 mi S (A). **SUMMIT**: Kamas 11 mi E (U), Park City (F), Wanship (US). **TOOELE**: Grantsville (US). **UINTAH**: Bonanza (KU). **UTAH**: Lehi (F), Provo (A), Thistle (F), and 7.7 mi E (A), Utah Lake (F). **WASATCH**: Bald Mt (KU), Francis 8.1 mi E, Hanna 3.6 mi W (A), Heber (F). **WASHINGTON**: locality unknown (F). **WAYNE**: Hanksville (BAD). **WEBER**: Ogden (F), Riverdale (US), Slaterville (F).

Smith (1979:1454) lists this species as eastren and western United States (no intermountain state is listed), where it nests in the soil, sometimes with loose mounds of soil and detritus, grasslands, and open woods. Hunt and Snelling (1975:23) list it from Arizona. Gregg (1963:529) lists it from Colorado between 3500 and 9000 ft under rocks and logs in a variety of habitats, predominantly in cottonwood-willow areas. La Rivers (1968:10) lists it from Nevada. Wheeler and Wheeler (1977) found it frequently in earthen mounds, also under rocks and wood in North Dakota. Cole (1942:383) indicates its habitat in Utah as soil, with numerous entrances in crude, flat, confluent craters. Knowlton (1975:3) found it associated with sagebrush and rabbitbrush in northern Utah.

Eighty ants in four collections were taken from under rocks. In one case they were under the same rock with *Formica pallidefulva* and once with *F. limata*. Ten ants in one collection were taken under the same log with *F. gnava* and *Camponotus modoc*. Fifteen ants in three collections were taken singly in open areas. Eggs were found under one rock in early July, and in mid-July many winged forms were found under a rock. These tried to hide and escape when disturbed. Two collections were in cottonwoods; one grass, herbs, and sagebrush; one herbs adjacent to a cultivated area; one Russian thistle; and one aspen and conifers. In 87 recorded Utah habitats it was taken 26 times in montane areas. In 49 recorded elevations between 4125 and 11,000 ft it was taken most frequently (44 times) under 6000. Beck et al. (1967:70) found it feeding on dead rodents in one instance in Utah.

Formica neogagates Emery

F. fusca subpolita var. *neogagates* Emery, 1893, Zool. Jahrb. Syst. 7:646.

F. neogagates: Rees and Grundmann 1940:10; Cole 1942:384; Hayward 1945:120; Creighton 1950:459; Ingham 1959:76; Knowlton 1970:209, 1975:3.

Records (Map 11): **BOX ELDER**: Beaver Dam (KU), Cedar Crk (City) (K70), Cedar Hill (KU), Curlew Jct (US), Hansel Mts (K75), Hardup (US), Kelton (K75), Kelton Pass, Locomotive Spngs (K70), Promontory Pt (C42), Snowville (K70) and 17 mi SW (KU), Taylor Farms (K75), Wildcat Hills (US). **CACHE**: Avon, Blacksmith Fk Cyn, Clarkston, Elk Valley, Green Cyn (KU), Logan, Logan Cyn (C42), Monte Cristo, Paradise, Petersboro, Providence, Tony Grove (KU). **CARBON**: Helper (KU). **EMERY**: Hideout Cyn nr Green River (U). **GARFIELD**: Boulder (U), Jct U12 and U63 0.5 mi E(A). **IRON**: Kanaraville (US). **JUAB**: Callao 5 mi E (A), Mt Nebo, Topaz Mt (KU). **MILLARD**: Tule Spngs, White Valley (C42). **PIUTE**: Marysvale 4.1 mi S (A). **RICH**: Monte Cristo, Randolph 10 mi SW (KU), Sage Crk Jct 5.1 mi W, Woodruff 4 mi W, Wyoming brdr 0.5 mi S on U16 (A). **SALT LAKE**: Alta, Cottonwood Cyn (C42), Red Butte Cyn (U), Salt Lake City (C42). **SANPETE**: Orangeville 19.5 mi W (A). **SEVIER**: Salina, Salina Cyn nr Fremont Jct (U), Sevier (C42). **TOOELE**: Lake Point (C42). **UTAH**: Aspen Grove (BY), Nibley, Spanish Fk Cyn (KU). **WASATCH**: Provo River N Fk (U). **WASHINGTON**: Hurricane (US), Kolob (I59), La Verkin (US), Rockville (KU), Santa Clara (US), St George (KU), Virgin River E Fk (I59). **WEBER**: Beaver Crk, Monte Cristo 6 mi S, Thomas Spng (KU).

Smith (1979:1450) lists this species from midwest to western United States, including Arizona, nesting under stones or in the open with or without a mound or crater in grasslands and dry situations. Gregg (1963:505) lists it from Colorado between 3500 and 9700 ft under rocks and in soil hummocks in a variety of habitats. Allred and Cole (1971:239) found it in Idaho in associations of wild ryegrass and rabbitbrush-sagebrush-grass-winterfat. In southern Nevada Cole (1966:26) found its nests under rocks in pinyon-juniper, and in Utah in small craters (1942:384). Wheeler and Wheeler (1963) found it frequently under rocks in North Dakota. Ingham (1959, 1963) found it under rocks and in small craters in open areas in oak, sagebrush, cultivated areas, shadscale, and greasewood in southern Utah. Knowlton (1975:3) found it associated with sagebrush, rabbitbrush, and sunflowers in northern Utah.

Seventy-eight ants in three collections were taken from moundless burrows. Twenty-one ants in two collections were taken from under rocks, once under the same rock with *Formica gnava*, *F. obscuripes*, and *F. perpilosa*. Nineteen ants in two collections were taken in the open. Five collections were in sagebrush: one in association with grass, one grass and herbs, and one grass and rabbitbrush. One collection was in grass and one in greasewood. In 65 recorded Utah habitats it was found 19 times in montane forest. In 32 recorded elevations between 2625 and 8585 ft it was taken most frequently between 4000 and 5000.

Formica neorufibarbis Emery

F. fusca var. *neorufibarbis* Emery, 1893, Zool. Jahrb. Syst. 7:646; Rees and Grundmann 1940:9; Cole 1942:382.

F. fusca gelida: Rees and Grundmann 1940:9; Cole 1942:382; Hayward 1945:120.

F. neorufibarbis: Grundmann 1958:166; Knowlton 1970:209, 1975:3; Francoeur 1973:225, 244.

F. neorufibarbis gelida: Beck et al. 1967:70.

Records (Map 11): **BOX ELDER**: Bear River City, Brigham, Collinston, Corinne, Curlew, Fielding, Garland, Hardup, Park Valley (City), Promontory Ridge, Riverside (= Belmont), Snowville, Thatcher, Tremonton, Willard (C42), Willard Basin (KU). **CACHE**: Amalga (C42), Franklin Basin (KU), Hyde Park, Lewiston, Logan, Logan Cyn (C42), Mendon, Monte Cristo (KU), Newton, Paradise, Petersboro, Richmond (C42), Ricks Spng (KU), Sardine Cyn, Smithfield (C42), Tony Grove Lake (KU), Trenton (C42), Wellsville (RG). **DAGGETT**: Green Lake (RG). **DAVIS**: Farmington, Farmington Cyn (KU), Kaysville (C42), Woods Cross (RG). **DUCHESNE**: Fruitland 4 mi W (U), Mirror Lake (KU).

GARFIELD: Osiris (U). **GRAND**: Moab (G58). **IRON**: Cedar City, Parowan, Summit (C42). **JUAB**: Callao (BAD). **KANE**: Orderville (G58). **MILLARD**: Holden, Leamington (C42). **RICH**: Allen Cyn (KU), Laketown (C42), Monte Cristo (KU). **SALT LAKE**: Butterfield Cyn, Hunter, Little Cottonwood Cyn, Mill Crk Cyn, Mt Dell Res (U), Murray (C42), Parleys Cyn (RG), Red Butte Cyn (U), Salt Lake City (C42). **SAN JUAN**: Angels Pk (KU), Blanding (G58), Geyser Pass (BAD), Monticello (G58). **SANPETE**: Ephraim (RG), Ephraim Cyn (KU). **SEVIER**: Salina (C42). **SUMMIT**: Henrys Fk Basin (RG), Kamas (C42), Park City (F), Wanship (C42). **TOOELE**: Fisher Pass, Grantsville, Iosepa, Orrs Ranch, St Johns (C42). **UINTAH**: Gusher (C42), Ouray (C42), Paradise Park, Vernal (U). **UTAH**: American Fk Cyn (U), Emerald Lake (BAD), Hobble Crk, Lehi, Orem, Provo (C42). **WASATCH**: Daniels Cyn, Deer Crk Res, Heber (U), Lost Lake (BY), Midway (U), Soapstone Cyn (RG). **WEBER**: Hooper, Ogden, Riverdale, Roy (C42). **COUNTY UNKNOWN**: Sharon (C42).

Smith (1979:1454) lists this species from midwest to western United States, including Arizona, nesting in rotting wood or under rocks in montane forest. Gregg (1963) lists it from Colorado between 6900 and 11,542 ft under rocks and logs and in hummocks predominantly in conifer habitats. Cole (1966:26) found its nests in southern Nevada under stones in pinyon-juniper, also in logs in wooded areas in Utah (1942:382). Wheeler and Wheeler (1978:395) found it between 6200 and 12,200 ft in Nevada, frequently in earthen mounds and under rocks and wood in North Dakota (1963). Grundmann (1958:166) indicates it as an inhabitant of cultivated and stream side areas usually below 5000 ft in Utah.

In 100 recorded Utah habitats 27 were in montane forest. In 71 elevations between 4042 and 11,300 ft, 52 were under 6000, 14 between 6000 and 8000, and one over 11,000. Beck et al. (1967:70) found it feeding on dead rodents in three instances in Utah.

Formica obscuripes Forel

F. rufa obscuripes Forel, 1886, Ann. Ent. Soc. Belg. 30:39; Rees and Grundmann 1940:8; Cole 1942:380.

F. rufa aggerans: Rees and Grundmann 1940:8.

F. rufa melanotica: Cole 1942:380.

F. obscuripes: Ingham 1959:80; Gregg 1963:570; Beck et al. 1967:70; Knowlton 1970:210, 1975:3; Smith 1979:1460.

Records (Map 12): **BOX ELDER**: Bear River City, Bear River Cyn, Brigham, Collinston, Garland, Honeyville (C42), Hansel Mts, Hardup, Kelton, Kelton Pass (K70), Promontory Pt, Raft River Mts (U), Snowville (K70), Wellsville Mts, Wildcat Hills (KU). **CACHE**: Amalga (C42), Ant Valley, Blacksmith Fk Cyn, Franklin Basin, W Hodges Cyn (KU), Logan, Logan Cyn (C42), Monte Cristo (KU), Providence, Smithfield (C42), Tony Grove Lake (KU). **DAGGETT**: Green Cyn (RG), Radosovich Ranch (BAD). **DAVIS**: Farmington, Layton (C42). **EMERY**: Carter Crk nr Green River (U). **GRAND**: La Sal Mts (BY), Warner Ranger Sta (Gr63). **JUAB**: McClellan Lake (KU), Nebo Loop rd 9.9 mi S Santaquin Cyn (A), Trout Crk (City) (C42). **MILLARD**: Swasey Spngs (RG). **MORGAN**: Morgan (C42). **PIUTE**: Marysvale 4.1 mi S (A). **RICH**: Meadowville 8 mi NW (KU), Monte Cristo Ranger Sta, Randolph (BAD) and 10 mi SW, Sage Crk (KU). **SALT LAKE**: Big Cottonwood Cyn (U), Holladay, Midvale, Murray, Parleys Cyn (C42), Red Butte Cyn (U). **SANPETE**: Fountain Green (C42), Wales (RG). **SEVIER**: Monroe Mt (BAD). **TOOELE**: Stansbury Island (C42), S Willow Cyn (U). **UINTAH**: Paradise Park 11 mi S (U). **UTAH**: Aspen Grove (BY), Lehi (RG), Provo (C42), Spanish Fk (BY), Spanish Fk Cyn (KU), Tibble Fk Cyn (A). **WASATCH**: Kamas 8 mi S (U). **WASHINGTON**: Harrisburg (C42), Pine Valley (City) (KU). **WAYNE**: Capitol Reef Nat Park (U). **WEBER**: Harrisville, Hooper, Huntsville, Ogden, Slaterville (C42), Woodruff 34.8 mi W (A).

Smith (1979:1460) lists this species from midwest to western United States, including Utah, nesting in large mounds of detritus in open areas. It is a known predator of the pine sawfly. Gregg (1963:570) lists it from Colorado between 3500 and 9500 ft under rocks and logs and in thatched domes in a variety of habitats, and gives a record for Utah. La Rivers (1968:10) lists it from Nevada, where Wheeler and Wheeler (1978:394) found it between 6400 and 10,500 ft. They found it frequently in thatched and duff mounds in North Dakota (1963). Cole (1942:380) indicates that its nests in Utah are domed mounds of detritus in open areas usually next to a shrub at lower elevations, or of mounds of detritus in areas of moderate to dense cover in aspen areas. Ingham (1959, 1963) found it in mounds of detritus in juniper in southern Utah. Knowlton (1975:3) found it associated with sagebrush, rabbitbrush, and sunflowers in northern Utah.

Four ants in one collection were taken from a mound of small sticks and soil next to a log in association with *Formica integroides* and *F. obscuriventris.* Ten ants in one collection were taken from a mound of sticks, and six ants in one collection were taken from under a rock where *F. gnava*, *F. neogagates*, and *F. perpilosa* also were found. Twenty-nine ants in three collections were taken in the open. Four collections were in sagebrush and two in aspen and fir. In 71 recorded Utah habitats it was taken 24 times in montane forest. In 40 recorded elevations between 3000 and 9100 ft it was taken most frequently between 4000 and 5000 (25 times) and 6000 and 9000 (14 times). Beck et al. (1967:70) found it feeding on dead rodents in four instances in Utah.

Formica obscuriventris Mayr

F. truncicola var. *obscuriventris* Mayr, 1870, Verh. Zool.-Bot. Ges. Wien 20:951.
F. truncicola obscuriventris: Rees and Grundmann 1940:8.
F. truncicola obscuriventris var. *aggerans*: Rees and Grundmann 1940:8.
F. rufa clivia: Cole 1942:380.
F. obscuriventris: Ingham 1959:80.
F. obscuriventris clivia: Smith 1979:1460.

Records (Map 11): **BOX ELDER**: Clear Crk (in Raft River Mts) (U), Mantua (KU), Promontory Pt (RG), Wellsville Mts, Willard Basin (KU). **CACHE**: Ant Valley, Blacksmith Fk Cyn, Hyrum (KU), Logan (C42), Logan Cyn, Mendon Cold Spngs, Millville, Providence, Rock Crk, Smithfield Cyn, Tony Grove (KU). **GRAND**: Moab (U). **IRON**: Cedar City (RAU). **KANE**: Long Valley Jct 11 mi W (I59). **RICH**: Meadowville Summit 8 mi W (KU). **SALT LAKE**: locality unknown (RG). **SANPETE**: Majors Flats (KU). **UINTAH**: Whiterocks (KU). **UTAH**: Payson Cyn 7.3 and 10.3 mi up, Santaquin 7.7 mi E, Tibble Fk Cyn (A). **WASATCH**: Francis 18.5 mi E, Hanna 14.3 mi W (A). **WEBER**: Slaterville (US).

Creighton (1950) and Smith (1979:1460) list two races of this species, *obscuriventris* and *clivia*, from eastern to western United States, including Utah and Colorado, nesting under logs and stones in grasslands, woods, and forests. Although both races have been recorded from Utah, the records probably are of *clivia*. Gregg (1963:572) lists the species between 5354 and 10,000 ft under rocks, logs, and in thatched domes in conifers, canyons, and pinyon-juniper-oak habitats in Colorado. Wheeler and Wheeler (1979:394) found it between 6300 and 10,000 ft in Nevada, and frequently in wood in North Dakota (1963). Cole (1942:380) indicates its habitats in Utah as under logs and stones in sparse to moderate cover. Ingham (1959) found it under logs in fir, aspen, and ponderosa pine in southern Utah.

Forty-nine ants in four collections were taken from under rocks, once under the same one with *F. subnitens*, once *F. lasioides*, and once *Lasius alienus* and *L. niger*. Eight ants in one collection were taken from a mound of small sticks and soil by a log in association with *F. integroides* and *F. obscuripes*. One ant was taken under the same log with *Camponotus modoc*, *F. podzolica*, and *F. subnitens*. Twenty-five ants were taken in the open. Six collections were in aspen: three in open meadows in association with fir, one with fir, and one with grass and herbs. One collection was in an association of herbs, oregon grape, shrubs, and fir. In 30 recorded Utah habitats it was taken 18 times in montane areas. In 11 known elevations between 4217 and 8100 ft it was taken most frequently under 5000, twice over 7000.

Formica obtusopilosa Emery

F. sanguinea obtusopilosa Emery, 1893, Zool. Jahrb. Syst. 7:643.
F. obtusopilosa: Cole 1942:377; Ingham 1963:104; Gregg 1963:610; Knowlton 1970:210, 1975:4; Allred and Cole 1979:98; Smith 1979:1450.

Records (Map 12): **BOX ELDER**: Bear River City, Blue Crk (City) (C42), Cedar Crk (City), Cedar Hill (K75), Curlew Jct (K70), Fielding, Garland (C42), Hansel Mts (K75), Hardup (C42), Kelton (US), Kelton Pass (K70), Portage (KU), Snowville (K70), Tremonton (C42). **CACHE**: Cache Jct, Green Cyn (C42), Hyde Park (KU), Logan (C42), Providence (KU), Richmond (US). **CARBON**: Helper (KU). **DUCHESNE**: Bonita (= Boneta), Duchesne (C42) and 2 mi N (A), Fruitland (C42). **EMERY**: Orangeville 14.3 mi W (A). **GRAND**: Thompson (C42). **IRON**: Cedar Valley (I59), Modena 5.3 mi W (A). **JUAB**: Ferno Valley (C42). **KANE**: Glen Cyn City (AC). **RICH**: Randolph 8 and 10 mi SW (KU). **SALT LAKE**: Dry Cyn, Salt Lake City (C42). **SAN JUAN**: La Sal Jct 1.6 mi S (A). **SANPETE**: Fairview 2 mi N (A). **TOOELE**: Gold Hill, Skull Valley, Stansbury Island, Timpie (C42). **UINTAH**: Bonanza 14 mi S (A), Dinosaur Nat Mon (Gr63), Lapoint (C42), Whiterocks (KU). **UTAH**: Lehi (C42), Spanish Fk Cyn (KU). **WEBER**: Jct U39 and U166 3.3 mi E (A). **COUNTY UNKNOWN**: Uinta (C42) (? = Uintah in Weber Co).

Smith (1979:1450) lists this species from midwest to western United States, including Utah and Nevada, nesting under stones or in open areas with irregular mounds or craters. Gregg (1963:610) lists it from Colorado between 4800 and 9500 ft under rocks and predominantly in grass and sagebrush habitats, and gives a record for Utah. Cole (1966:26) found its nests in southern Nevada in soil without mounds in desert shrub habitats. Wheeler and Wheeler (1963) found it frequently under rocks in North Dakota. Allred and Cole (1979:98, 1971:239) found it in southern Utah and Idaho in associations of ephedra-grass, sagebrush-grass, and goosefat-winterfat. Cole (1942:378) indicates that in Utah it nests in obscure craters, under stones, or in soil without craters in grassy areas. Ingham (1963) found it in juniper, sagebrush, and greasewood in southern Utah. Knowlton (1975:4) found it associated with rabbitbrush, sunflowers, and shadscale in northern Utah.

There were 109 ants in five collections taken from small crater mounds about one inch high and six inches in diameter. Twenty ants in one collection were taken from under a rock, and 5 ants in one collection singly in an open area. One of the mound colonies contained eggs, larvae, and pupae in late July. Five collections were in sagebrush: two in association with grass and one with herbs. One collection was in a grass, juniper, and pinyon association. In 48 recorded Utah habitats it was taken only 4 times in montane areas. In 25 recorded elevations between 3250 and 7000 ft it was taken most frequently between 4000 and 6000.

Formica occulta Francoeur

F. occulta Francoeur, 1973, Soc. Ent. du Quebec, Mem. 3, p. 94; Smith 1979:1454.

Records (Map 11): **BOX ELDER**: Willard Basin (KU). **CACHE**: Ant Valley, Antelope Valley, Blacksmith Fk Cyn L Fk, Franklin Basin, Tony Grove, Logan Cyn (KU). **EMERY**: Joes Valley (U). **RICH**: Randolph 10 mi SW, Sage Crk, Sage Crk Jct (KU). **SEVIER**: Fremont 9.7 mi N (A). **SUMMIT**: Wyoming brdr on U150 (A). **WASATCH**: Hanna 9.2 mi W (A).

Smith (1979:1454) lists this species from western United States, including Utah, Colorado, Arizona, and Wyoming.

Thirty-five ants in three collections were found under rocks, once in association with *F. limata*. Three collections were in sagebrush, once in association with matchbrush. In 14 recorded Utah habitats it was taken in montane areas nine times. Five recorded elevations were between 6260 and 9300 ft, mostly above 8000.

Formica opaciventris Emery

F. exsectoides var. *opaciventris* Emery, 1893, Zool. Jahrb. Syst. 7:643.

Records: **CACHE**: Blacksmith Fk Cyn, Elk Valley, Franklin Basin, Tony Grove Lake (KU).

Smith (1979:1456) lists this species from midwest to western United States, including Colorado and Wyoming, nesting in earthen or thatched mounds. Gregg (1963:601) lists it between 5160 and 10,500 ft in thatched domes from sagebrush to conifer habitats in Colorado.

Formica oreas Wheeler

F. oreas Wheeler, 1903, Bull. Amer. Mus. Nat. Hist. 19:643; Rees and Grundmann 1940:9; Cole 1942:379; Ingham 1959:80; Knowlton 1975:4.

F. oreas comptula: Rees and Grundmann 1940:9; Cole 1942:380; Smith 1979:1461.

F. oreas oreas: Smith 1979:1461.

Records (Map 12): **BOX ELDER**: Bear River, Clear Crk, Hansel Mts (KU), Kelton (US), Kelton Pass (K75), Snowville, Willard Basin (KU). **CACHE**: Avon, Beaver Crk (KU), Blacksmith Fk (RG), Carter Crk (KU), Cornish (RG), Cove (C42), Franklin Basin, High Crk, Leeds Cyn (KU), Logan (C42), Logan Cyn, Tony Grove Cyn (KU). **DUCHESNE**: Wolf Crk (RG). **KANE**: Duck Crk on Cedar Mt (I59). **RICH**: Allen Cyn, Sunrise Cmpgnd (KU). **SALT LAKE**: Big Cottonwood Cyn, Butterfield Cyn, Red Butte Cyn, Rose Cyn (U). **SAN JUAN**: Hole-in-the-Rock Cyn (U). **UINTAH**: Dry Fk rd 15 mi N U121 (A). **UTAH**: Diamond Fk Cyn, Spanish Fk Cyn (KU), Thistle 14.6 and 20.4 mi E (A). **WASATCH**: Soldier Summit 1 mi E (A). **WASHINGTON**: St George (RG). **COUNTY UNKNOWN**: Duck Crk in Cedar Mts (RG).

Creighton (1950) and Smith (1979:1461) list two races of this species from midwest to western United States, including Utah, Colorado, and Wyoming, nesting under logs or stones banked with detritus in open woods, meadows, or grasslands. Both races have been recorded from Utah. They may be separated by the color of the head and thorax, which in *oreas* are clear red, and in *comptula* are deep brown. Gregg (1963:577) lists this species between 5200 and 10,505 ft under rocks in a variety of habitats in Colorado. Wheeler and Wheeler (1978:394) found it between 6400 and 8800 ft in Nevada, frequently in wood and commonly in duff-covered mounds in North Dakota (1963). Allred and Cole (1971:239) found it in Idaho in associations of rabbitbrush-sagebrush-grass and wild ryegrass. Cole (1942:379) indicates its habitat in Utah as under stones banked with detritus in open sunny areas. Ingham (1959) found it in mounds of detritus in southern Utah. Knowlton (1975:4) found it associated with rabbitbrush in northern Utah.

Fifty ants in two collections were taken from low mounds of sticks, both times in association with *F. integroides*. Twenty ants in two collections were taken singly in open areas. Four collections were in sagebrush: one in association with herbs; one grass and rabbitbrush; one grass, clover, and Russian thistle; and one grass, aspen, and pine. In 36 recorded Utah habitats it was taken 23 times in montane forest. In 15 recorded elevations between 2760 and 9300 ft it was taken most frequently between 4000 and 5000 ft.

Formica pallidefulva Emery

F. pallide-fulva nitidiventris Emery, 1893, Zool. Jahrb. Syst. 7:645; Rees and Grundmann 1940:10.

F. pallidefulva nitiventris: Ingham 1959:85.

F. pallidefulva: Knowlton 1975:4.

Records (Map 12): **BOX ELDER**: Wildcat Hills (K75). **GRAND**: La Sal Mts (KU). **JUAB**: Nebo Loop rd 9.9 mi S Santaquin Cyn (A). **SALT LAKE**: Parleys Cyn (RG). **UINTAH**: Red Cloud Loop rd 9.2 mi W U44 (A). **WASATCH**: Francis 8.1 mi E (A). **WASHINGTON**: Zion Nat Park (I59).

Creighton (1950) and Smith (1979:1451) list two forms of this species from eastern to western United States, including Colorado and Wyoming. The Utah subspecies probably is *nitidiventris*, which can be distinguished from *pallidefulva* by the clear golden yellow color of *pallidefulva* as contrasted with the yellowish to blackish brown of *nitidiventris*. Gregg (1963:627) lists this species between 3500 and 8000 ft under rocks in a variety of habitats in Colorado. Ingham (1959) found it under rocks in ash, oak, poplar, and poison ivy in southern Utah. Knowlton (1975:4) found it associated with sagebrush in northern Utah.

Fifty ants in two collections were taken from under rocks, once under the same one with *F. neoclara*, and once with *F. argentea* and *Pheidole desertorum*. Three ants in one collection were taken singly in an open area. One collection was in sagebrush, one cottonwoods, and one a grassy meadow. In seven recorded Utah habitats five were in montane areas. One recorded elevation is 4500 ft.

Formica pergandei Emery

F. pergandei Emery, 1893, Zool. Jahrb. Syst. 7:643.

Record: **UINTAH**: Whiterocks Cyn (KU).

Smith (1979:1464) lists this species from eastern to western United States, including Colorado, frequently associated with *F. fusca* and *F. pallidefulva*.

Formica perpilosa Wheeler

F. fusca subpolita var. *perpilosa* Wheeler, 1902, Mem. Revist. Soc. Sci. Ant. Alzate 17:141.

F. perpilosa: Rees and Grundmann 1940:8; Cole 1942:378; Grundmann 1958:166; Ingham 1959:77; Beck et al. 1967:70.

Records (Map 13): **EMERY**: San Rafael River (BAD). **KANE**: Cottonwood Cyn (BAD), Glendale, Kanab, Orderville (C42). **MILLARD**: Sutherland (US). **PIUTE**: Marysvale 4.1 mi S (A). **SALT LAKE**: Salt Lake City (RG). **TOOELE**: Stansbury Island (RG). **UINTAH**: Jensen (U). **WASHINGTON**: Grafton (I59), Hurricane (RG), Rockville (I59), Santa Clara (C42), Springdale (I59), St George (C42), Washington (KU). **WAYNE**: Pleasant Crk (BAD).

Smith (1979:1450) lists this as a midwestern and western species, including Colorado and Wyoming, which usually constructs crater nests in grasslands and open fields. Hunt and Snelling (1975:23) list it from Arizona. Gregg (1963:611) lists it between 3500 and 6000 ft under wood and in dome nests in a variety of habitats in Colorado. La Rivers (1968:10) lists it from Nevada. Cole (1942:378) states that in Utah its nests are obscure craters or low domes around the roots of trees and shrubs, particularly in irrigated areas and dry river beds. Grundmann (1958:166) indicates that its nests in Utah are obscure and difficult to find, consisting of mounds around the bases of shrubs and trees along stream banks. Ingham (1959, 1963) found it in southern Utah under wood, in small half-moon-shaped mounds, and in clumps of grass in willow, tamarix, poplar, and alkali flats.

One ant was collected from under a rock in sagebrush. Ants of *F. gnava*, *F. neogagates*, *F. obtusopilosa*, and *F. perpilosa* were under the same rock. In 18 recorded Utah habitats only one was in a montane area. Twenty-one collections at known elevations were about equally distributed between 2625 and 6600 ft. Beck et al. (1967:70) found it feeding on dead rodents in three instances in Utah.

Formica podzolica Francoeur

F. podzolica Francoeur, 1973, Ent. Soc. Quebec, Mem. 3:167.

Records (Map 13): **BEAVER**: Beaver (F). **BOX ELDER**: Cedar Hill (US), Clear Crk (in Raft River Mts) (U), Snowville (US), Willard Pk (KU). **CACHE**: Ant Valley, Bear River Mts, Blacksmith Fk Cyn, Franklin Basin, Green Cyn, Hodges Cyn, Hyrum, Logan (KU), Logan Cyn (US), Millville, Providence, Tony Grove (KU), Wellsville Mts (US). **CARBON**: Clear Crk Cyn (F), Scofield 5.2 mi SW, Scofield Res 4 mi S, Wellington 12 mi NE (A). **DAVIS**: Farmington (KU), Farmington Cyn (US). **IRON**: Upper Bear Crk, Cedar City (RAU) and 19 mi E (A), Summit Crk (RAU). **JUAB**: Lynndyl 11.5 mi N (A), Toms Crk (in Deep Crk Mts) (U). **RICH**: Allen Cyn (F), Meadowville, Monte Cristo, Pickleville (KU). **SAN JUAN**: Elk Ridge, Kigalia Ranger Sta (F). **SUMMIT**: Mirror Lake 11.6 and 17.3 mi N (A). **TOOELE**: Dugway 11.9 mi E (A), Willow Cyn (F). **UINTAH**: Dry Fk rd 15 mi N U121, Red Cloud Loop rd 4.2 and 9.2 mi W U44 (A), Whiterocks (F). **UTAH**: Mt Nebo (F), Payson Cyn 12.3 mi up, Santaquin Cyn 4.5, 6.7, 7.1 and 7.7 mi up (A), Thistle (F), Tibble Fk Cyn, Tibble Fk Lake 2.3 mi W (A). **WASATCH**: Francis 8.1 and 18.5 mi E, Hanna 14.3 mi W, Midway 3.7 mi NW, Soldier Summit 1 mi E and 10.1 mi N (A). **WEBER**: Beaver Crk (KU). **COUNTY UNKNOWN**: Beaver Head (KU), Chalk Crk (F) (in either Millard or Summit Co).

Smith (1979:1455) lists this species from eastern to western United States, including Arizona, nesting in soil mounds in montane forest.

There were 123 ants in 10 collections taken from under rocks, once under the same one with *F. gnava*, once *F. fusca*, once *F. moki*, once *F. limata*, and once *F. fusca* and *Solenopsis molesta*. There were 171 ants in 6 collections taken from ground burrows, only 2 of which had low mounds. Twenty-three ants in 4 collections were taken from under logs, once under the same log with *F. fusca* and *F. gnava*, once *Camponotus modoc*, and once *C. modoc*, *F. obscuriventris*, and *F. subnitens*. Thirty ants in one collection were taken from inside a log. Forty-nine ants in 6 collections were taken singly in open areas. Immatures were found in a burrow in late June and under a rock in early August. Sixteen collections were from aspen: 4 in association with grass, herbs, and shrubs; three sagebrush and conifers; one grass; one herbs in an open meadow; one chokecherry; one chokecherry and fir; one maple, oak, and fir; and one pine. Two collections were in grass and herbs, one juniper and pinyon, two fir, one oak, and one sagebrush and herbs. In 62 recorded Utah habitats 41 were in montane forest. In 15 recorded elevations between 4302 and 9300 ft it was taken 11 times under 6000. In one instance, when a cover rock was removed to expose the ants, they ran rapidly and tried to escape. In another case, when the burrow was excavated, the ants scurried around but did not leave the area. Many of them worked furiously to remove the few exposed pupae.

Formica puberula Emery

F. sanguinea puberula Emery, 1893, Zool. Jahrb. Syst. 7:643; Rees and Grundmann 1940:8; Cole 1942:378; Knowlton 1970:210.

F. puberula: Creighton 1950:468; Gregg 1963:614; Knowlton 1975:4.

Records (Map 13): **BOX ELDER**: Snowville (K75). **GRAND**: Warner Ranger Sta (Gr63). **PIUTE**: Fish Lake Jct 1 mi S (U). **SAN JUAN**: La Sal Mts (RG). **SANPETE**: Ephraim Cyn (KU), Wales (RG). **TOOELE**: Stockton (RG). **UINTAH**: Paradise Park 11 mi S (U).

Smith (1979:1465) lists this species from midwest and western United States, including Colorado and Wyoming, where it frequently associates with as many as 12 species of *Formica*. Gregg (1963:614) lists it between 5100 and 10,000 ft under rocks and logs predominantly in conifer habitats in Colorado, and gives a record for Utah. La Rivers (1968:10) lists it from Nevada, where Wheeler and Wheeler (1978:396) found it between 6400 and 8200 ft. Cole (1942:378) indicates that it nests under stones in Utah. In seven recorded Utah habitats it was found three times in montane areas. Three known elevations are 4544, 5069, and 8000 ft.

Formica querquetulana Kennedy and Dennis

F. querquetulana Kennedy and Dennis, 1937, Ann. Ent. Soc. Amer. 30:536.

Record: **CACHE**: Leeds Cyn (KU).

Smith (1979:1463) lists this species from eastern United States. Its occurrence in Utah is questionable.

Formica rasilis Wheeler

F. microgyna var. *rasilis* Wheeler, 1903, Bull. Amer. Mus. Nat. Hist. 19:648.

F. microgyna rasilis: Rees and Grundmann 1940:9; Cole 1942:381.

F. rasilis: Creighton 1950:506; Gregg 1963; Knowlton 1975:5; Smith 1979:1463.

Records (Map 13): **BOX ELDER**: Snowville (K75). **CACHE**: Bear River Mts (KU). **GARFIELD**: Bryce Cyn Nat Park (Cr). **GRAND**: Warner Ranger Sta (Gr63). **SALT LAKE**: Butterfield Cyn, Red Butte Cyn (U). **SAN JUAN**: La Sal Mts (RG).

Smith (1979:1463) lists this species from western United States, including Utah and Colorado, nesting under stones in open areas. Gregg (1963) lists it between 5400 and 11,542 ft under rocks and logs and in thatched nests predominantly in conifer habitats in Colorado, and gives a record for Utah.

La Rivers (1968:10) lists it from Nevada. Cole (1942:381) indicates its habitat in Utah as under stones frequently banked with detritus. In six recorded Utah habitats five were in montane areas. Six recorded elevations were between 4544 and 8000 ft.

Formica subintegra Emery

F. sanguinea rubicunda var. *subintegra* Emery, 1893, Zool. Jahrb. Syst. 7:643.

Records: **BOX ELDER**: Hansel Mts (KU). **RICH**: Monte Cristo (KU). **SANPETE**: Ephraim Cyn (KU).

Smith (1979:1465) lists this species from eastern to midwestern United States. No intermountain state is listed, and its occurrence in Utah is questionable.

Formica subnitens Creighton

F. rufa subnitens Creighton, 1940, Amer. Mus. Nat. Hist. Nov. 1055:7.

F. subnitens: Knowlton 1970:210, 1975:5.

F. subaenescens: Knowlton 1975:5.

Records (Map 14): **BOX ELDER**: Hardup, Snowville (K70) and 9 mi W (US). **CACHE**: Elk Valley, Leeds Cyn, Logan Cyn, Rock Crk (in Blacksmith Fk Cyn), Tony Grove Cyn (KU). **IRON**: Upper Bear Crk (RAU). **RICH**: Sage Crk Jct 5.1 mi W (A). **UINTAH**: Dry Fk rd 15 mi N U121, Red Cloud Loop rd 4.2 mi W U44 (A). **UTAH**: Halls Fk rd 8.8 mi N Hobble Crk rd, Payson Cyn 10.3 mi up, Santaquin Cyn 7.7 mi up (A). **WASATCH**: Midway 5.7 and 11.6 mi W, Soldier Summit 3.3 mi N, Strawberry Res 4 mi S (A).

Smith (1979:1461) lists this species from midwest to western United States, including Colorado and Wyoming, nesting under stones or in mounds of thatch. Gregg (1963:581) lists it at 6100 ft in thatched nests in pinyon-juniper in Colorado. Wheeler and Wheeler (1963) found it in thatched mounds in North Dakota.

Seventy-five ants in three collections were taken from mounds of sticks, once next to a boulder and once at the base of a stump. One ant was taken from under the same log as *F. obscuriventris*, *F. podzolica*, and *Camponotus modoc*. Eleven ants in two collections were taken from under rocks, once under the same rock with *F. obscuriventris*. Thirteen ants in four collections were taken singly in open areas. Eggs were found in one mound in late July. Five collections were in aspen: one in association with grass and herbs; one grass, herbs, shrubs, and fir; one grass, sagebrush, and pine; one chokecherry; and one fir. Two collections were in grass, herbs, and sagebrush; one legumes and sagebrush; one matchbrush and sagebrush; and one oak and fir. In 19 recorded Utah habitats it was taken 15 times in montane areas. One recorded elevation was 4544 ft. Ants on a mound of thatched soil were highly defensive, rearing back in a position of defense to await an invader.

Formica subnuda Emery

F. sanguinea rubicunda var. *subnuda* Emery, 1895, Zool. Jahrb. Syst. 8:335.

F. sanguinea subnuda: Rees and Grundmann 1940:8; Cole 1942:378; Hayward 1945:120; Creighton 1950:469.

F. subnuda: Ingham 1959:79; Gregg 1963:620.

Records (Map 14): **BOX ELDER**: Snowville (C42). **CACHE**: Tony Grove (KU). **CARBON**: Scofield 4 mi S (A). **GARFIELD**: Boulder Mt (U), Bryce Cyn Nat Park (WU). **GRAND**: Warner Ranger Sta (Gr63). **IRON**: Cedar Breaks Nat Mon (159), Cedar City 14 mi E (A). **KANE**: Cedar City 24.3 mi E (A). **SALT LAKE**: Big Cottonwood Cyn, Red Butte Cyn (U). **SAN JUAN**: La Sal Mts (C42), Monticello 5 mi W (U). **SANPETE**: Orangeville 23.9 mi W (A), Wales (C42). **SUMMIT**: Kamas 11 mi E (U), Kamas 21 and 28.5 mi E (A), Soapstone Cyn (RG). **TOOELE**: Grantsville, Stockton, Tooele (C42). **UINTAH**: East Pk Res rd 2 mi W U44 (A), Trial Lake (U). **UTAH**: Aspen Grove, Provo Cyn (U), Silver Lake Flat (A). **WASATCH**: Horse Crk (C42), Midway 11.6 mi W, Soldier Summit 7.9 mi N (A). **WAYNE**: Capitol Reef Nat Park (U), Henrys Fk Basin (RG). **COUNTY UNKNOWN**: Pallisade Park (in Ashley Nat Forest) (RG).

Smith (1979:1465) lists this species from eastern to western United States, including Colorado and Arizona, frequently associated with *F. altipetens*, *F. fusca*, *F. neorufibarbis*, and *F. subpolita*. Gregg (1963:620) lists it between 5000 and 13,000 ft under rocks and logs and in thatched nests in a variety of habitats in Colorado, and gives a record for Utah. La Rivers (1968:11) lists it from Nevada, where Wheeler and Wheeler (1978:396) found it between 8200 and 11,000 ft. They found it frequently in wood, also common under rocks and in earthen mounds in North Dakota (1963). Cole (1942:378) indicates it nests under stones and logs in Utah. Ingham (1959) found it under stones and logs in fir, spruce, aspen, and pine in southern Utah.

There were 244 ants in nine collections found under logs, once under the same one with *F. fusca*, once *F. gnava*, and once *F. manni*. Fifteen ants in one collection were found inside a decaying log. These tried to escape when disturbed, crawling under debris. One ant next to the log had a struggling carabid beetle in its jaws, carrying it toward the log. Sixteen ants in one collection were taken singly in an open area. Eggs were found under one log in mid-July. Ants associated with these eggs held firmly onto the substrate and reared back in a biting position when disturbed. Eight collections were in aspen: one in association with grass; one grass, herbs, and pine; two conifers; and one chokecherry. Three collections were in conifers. In 32 recorded Utah habitats it was taken 26 times in montane forest. In 15 recorded elevations between 4304 and 10,500 ft it was taken more frequently above 7000.

Formica subpolita Mayr

F. fusca var. *subpolita* Mayr, 1886, Verh. Zool.-Bot. Ges. Wien 36:426.

F. subpolita cemponoticeps: Rees and Grundmann 1940:10; Cole 1942:384; Ingham 1959:84; Knowlton 1970:210, 1975:5.

F. subpolita: Cole 1942:383; Ingham 1959:83.

F. subpolita ficticia: Creighton 1950:542.

Records (Map 14): **BOX ELDER**: Bear River City, Blue Crk (City), Cosmo (? = Kosmo), Hardup, Kelton, Locomotive Spngs, Park Valley, Penrose, Rosette, Snowville, Willard (C42). **CACHE**: Logan, Logan Cyn, Trenton (C42). **EMERY**: San Rafael Swell (US). **GRAND**: Moab (RG). **JUAB**: Diamond Cyn, Nephi (C42). **MILLARD**: Delta (C42), Swasey Spngs (RG). **SALT LAKE**: Ft Douglas (C42). **SAN JUAN**: Blanding (C42), La Sal Mts (U). **TOOELE**: Clover, Fisher Pass, Flux, Grantsville, Iosepa, Orrs Ranch, Stansbury Island (C42). **UTAH**: Provo (C42). **WASHINGTON**: Hurricane (RG), Pine Valley (City) (159), St George (C42). **WEBER**: Ogden (C42). **COUNTY UNKNOWN**: Rosebud, Showell, Westpoint (C42).

Smith (1979:1455) lists this species from western United States, including Nevada and Idaho, nesting in mounds or craters in semidesert areas. Gregg (1963:541) lists it from Colorado between 5300 and 7800 ft. Wheeler and Wheeler (1978:396) found it between 6000 and 10,800 ft in Nevada. Allred and Cole (1971:239) found it in Idaho in associations of a variety of shrubs. Cole (1966:26) found its nests in southern Nevada under stones commonly in pinyon-juniper; also in grassy areas in Utah (1942:384). Ingham (1959, 1963) found it under stones in juniper and sagebrush in southern Utah. Knowlton (1975:5) found it in northern Utah.

In 38 recorded Utah habitats it was taken only 3 times in montane areas. In 28 recorded elevations between 2700 and 9000 ft it was taken most frequently between 3000 and 4000, twice over 7000.

Formica subsericea Say

F. subsericea Say, 1836, Boston J. Nat. Hist. 1:289.

Records: **CACHE**: Logan Cyn, Wellsville (US). **SEVIER**: Richfield (US).

Smith (1979:1455) lists this species from eastern to midwestern United States, but does not include an intermountain one. Wheeler and Wheeler (1978:396) found it between 7000 and 11,500 ft in Nevada, and frequently in earthen mounds, under rocks, and in and under wood in North Dakota (1977). Utah records of this species were taken at 4495 and 5340 ft. According to Snelling (pers. comm.) these Utah records are probably based on misidentifications.

Formica transmontanis Francoeur

F. transmontanis Francoeur, 1973, Soc. Ent. du Quebec, Mem. 3:35.

Record: **SAN JUAN**: Monticello (KU).

Smith (1979:1455) lists this species from western United States, including Idaho.

Formica wheeleri Creighton

F. wheeleri Creighton, 1935, Amer. Mus. Nat. Hist. Nov. 773:1; Rees and Grundmann 1940:10; Cole 1942:378; Creighton 1950:472; Grundmann 1958:166; Smith 1979:1466.

Records: **GRAND**: Warner Ranger Sta (RG). **SAN JUAN**: Blue Mts (C42) (? = Abajo Mts).

Smith (1979:1466) lists this species from midwest and western United States, including Utah, Colorado, and Arizona, associated with *F. altipetens*, *F. fusca*, *F. lasioides*, *F. neogagates*, and *F. neorufibarbis*. Gregg (1963:623) lists it between 5500 and 9500 ft under rocks in several habitats in Colorado. Wheeler and Wheeler (1963) found it under rocks and in earthen mounds in North Dakota. Cole (1942:378) states that it nests under stones on open hillsides in aspen forests in Utah, where it takes *F. lasioides* as a slave species (Grundmann 1958:166).

Formica whymperi Wheeler

F. adamsi var. *alpina* Wheeler, 1909, J. New York Ent. Soc. 17:85.

F. whymperi alpina: Creighton 1950:509; Gregg 1963:593; Smith 1979:1463.

Record: **GRAND**: Warner Ranger Sta (Gr63).

Creighton (1950) and Smith (1979) list four races of this species from midwest to western United States, including Utah, Colorado, and Idaho, nesting under stones or logs in forest areas, where it associates with *F. neoclara* and *F. neorufibarbis*. The subspecies in Utah is likely *alpina*. Gregg (1963:593) lists it between 8500 and 12,500 ft under rocks and logs and in thatched nests in conifer habitats in Colorado, and gives a record for Utah. Allred and Cole (1971:239) found it in associations of rabbitbrush-sagebrush-grass-winterfat in Idaho.

Formica xerophila M. R. Smith

F. moki xerophila Smith, 1939, Ann. Ent. Soc. Amer. 32:583.

F. moki: Rees & Grundmann 1940:10; Ingham 1959:84.

F. xerophila: Francoeur 1973:262; Smith 1979:1455.

Records (Map 14): **BEAVER**: Milford (RG). **DAVIS**: Farmington Cyn (KU). **SALT LAKE**: Big Cottonwood Cyn, Mt Olympus (U), Parleys Cyn (Cr). **SAN JUAN**: Blanding, Bluff (RG). **UINTAH**: Red Cloud Loop rd 4.2 mi W U44 (A). **WASHINGTON**: Big Plains, Central, Zion Nat Park (I59).

Smith (1979:1455) lists this species from western United States, including Utah and Arizona. In 12 recorded Utah habitats 5 were in montane areas. Fourteen recorded elevations were between 4000 and 7000 ft, 6 under 5000.

Formicoxenus chamberlini (Wheeler)

Symmyrmica chamberlini Wheeler, 1904, Bull. Amer. Mus. Nat. Hist. 20:5; Rees and Grundmann 1940:6; Cole 1942:370; Creighton 1950:281; Smith 1979:1398.

Records: **SALT LAKE**: Salt Lake City (RG). **SAN JUAN**: Blanding 8 mi N (U).

Smith (1979:1398) lists this species as Utah and Oregon, nesting with *Manica mutica*.

Hypoponera opaciceps (Mayr)

Ponera opaciceps Mayr, 1887, Verh. Zool.-Bot. Ges. Wien 37:536; Grundmann 1958:161; Ingham 1963:39.

Records: **SALT LAKE**: Salt Lake City (U). **WASHINGTON**: St George (I59).

According to Smith (1979:1343), this is primarily an eastern species ranging westward to Arizona and Colorado. Gregg (1963:284) found it between 5354 and 5400 ft in cottonwood-willow habitats in Colorado. La Rivers (1968:2) listed it from Nevada. Grundmann (1958:161) indicates that in Utah it ranges up to 4000 ft in dry desertlike areas where there is moisture, and nests under stones among willows. Four known elevations in Utah are from 2700 to 4453 ft.

Hypoponera opacior (Forel)

Ponera trigona var. *opacior* Forel, 1893, Trans. Ent. Soc. London, p. 363; Cole 1942:359.

Records: **SALT LAKE**: Salt Lake City (U). **UTAH**: Springville (C42).

Smith (1979:1343) lists this species from eastern to western United States, including Colorado. Hunt and Snelling (1975:20) list it from Arizona. Gregg (1963:286) lists it between 4000 and 5400 ft under rocks in grassy habitats in Colorado. One Utah collection was taken at 4253 ft.

Iridomyrmex humilis (Mayr)

Hypoclinea humilis Mayr, 1868, Soc. Nat. Modena, Ann. 3:164.

Records: **GRAND**: Moab (U). **SAN JUAN**: Goulding Trading Post (U).

Smith (1979:1418) lists this species from eastern to western United States, including Arizona, nesting in soil, rotting wood, or debris. La Rivers (1968:6) lists it from Nevada. Elevation of two recorded Utah collections was 4000 ft.

Iridomyrmex pruinosus (André)

Tapinoma anale André, 1893, Rev. Ent. de France 12:148.

I. pruinosus: Rees and Grundmann 1940:7; Cole 1942:373; Allred and Cole 1979:98.

I. analis: Rees and Grundmann 1940:6.

I. pruinosus analis: Rees and Grundmann 1940:7; Cole 1942:373; Grundmann 1958:165; Ingham 1959:62; Beck et al. 1967:70.

I. pruinosus testaceus: Cole 1942:373.

Records (Map 15): **BOX ELDER**: Bovine (C42), Brigham (A), Lucin, Park Valley (City) (C42). **CACHE**: Green Cyn (KU), Logan Cyn (C42), Tony Grove (KU). **DUCHESNE**: Roosevelt (C42). **EMERY**: Greenriver (US), Wellington 46 mi S (A). **GRAND**: Dewey (U), Moab (C42). **JUAB**: Chicken Crk Res (KU). **KANE**: Castle Rock (U), Coral Pink Sand Dunes (I59), Glen Cyn City (AC), Kanab (C42). **MILLARD**: Deseret (C42). **SALT LAKE**: Big Cottonwood Cyn (C42), Butterfield Cyn (U), S Dry Cyn, Ft Douglas (C42), Mt Olympus (U), Parleys Cyn (C42). **SAN JUAN**: Bluff (BAD), Johns Cyn (RG), La Sal (C42), Monticello (U), Montezuma Crk (BAD), Monument Valley (KU). **SEVIER**: Salina Cyn nr Fremont Jct (U). **TOOELE**: Clover, Iosepa (C42). **UINTAH**: Gusher (C42). **UTAH**: Aspen Grove (BY), Pelican Pt (RG). **WASHINGTON**: Harrisburg (US), Harrisburg Jct (I59), Hurricane (US), La Verkin, Pintura, Rockville, Veyo, Virgin City (I59), Zion Nat Park (C42). **WAYNE**: Fruita 5 mi SE (U), Hanksville 17 mi S (KU). **COUNTY UNKNOWN**: Valley Jct, Willow Spngs (C42).

Snelling (pers. comm.) indicates that this is a *Forelius*, but for the present I am retaining it as indicated.

Creighton (1950) and Smith (1979:1419) indicate two races of this species as midwest and western in the United States, including Idaho, where nests are under objects or in craterlike mounds in open areas. The Utah population, probably the subspecies *analis*, can be separated from *pruinosus* by the dense pubescence on the head and thorax of *pruinosus* that partially obscures its rough surface, whereas on *analis* the pubescence is dilute and reveals the shining surface beneath. Hunt and Snelling (1975:22) list it from Arizona. Gregg (1963:436) lists it from Colorado between 3500 and 6300 ft under rocks in a variety of habitats, predominantly pinyon-juniper and grass. Cole (1966:18) states that in southern Nevada it nests under stones, at the base of plants, and in mounds in open areas in a variety of desert shrub habitats. He found it in Utah in craterlike nests in sandy soil (1942:373). Wheeler and Wheeler (1963) found it in soil craters in North Dakota. Grundmann (1958:165) indicates that nests of these ants in Utah are difficult to locate, and occur most commonly in grass habitats near desert mountains. Ingham (1959, 1963) found it under stones and in small craters in creosote bush, sagebrush, pinyon-juniper, galletagrass, rabbitbrush, winterfat, joshua trees, four-wing saltbush, and shadscale in southern Utah. Allred and Cole (1979:98) found it in southern Utah in a variety of desert shrub types, most commonly in sagebrush.

Sixty ants in two collections were taken from small mounds with a central top opening. These ants are rapid runners. One collection was in halogeton and one in sunflowers, sagebrush, and rabbitbrush. In 49 reported habitat localities this species was taken 10 times in montane areas. In 45 recorded elevations between 2500 and 8100 ft it was taken 29 times between 3000 and 5000, 14 times between 5000 and 8000. Beck et al. (1967:70) found it feeding on dead rodents in three instances in Utah.

Lasius alienus (Foerster)

Formica aliena Foerster, 1850, Hymenop. Studien (Ernst Ter Meer Publ. Aachen) 1:36.

L. niger alienus var. *americanus*: Rees and Grundmann 1940:7.

L. niger var. *americanus*: Rees and Grundmann 1940:7; Cole 1942:374; Knowlton 1970:210.

L. alienus americanus: Grundmann 1958:166; Ingham 1959:72; Knowlton 1970:210, 1975:5.

L. alienus: Beck et al. 1967:70.

Records (Map 15): **BOX ELDER**: Kelton, Kelton Pass (K70), Snowville (C42), Willard Basin (KU). **CACHE**: Ant Valley, Beaver Crk (KU), Blacksmith Fk Cyn, Cowley Cyn (C42), Franklin Basin, W Hodges Cyn (KU), Logan Cyn (C42), Tony Grove Lake (KU). **DUCHESNE**: Duchesne (C42). **EMERY**: Hideout Cyn nr Green River (U). **GARFIELD**: Boulder Mt, Henry Mts (G58), Osiris (U). **GRAND**: Thompson (KU). **IRON**: Coal Crk Cyn (I59). **KANE**: Kanab and 20 mi N (C42). **MILLARD**: locality unknown (RG). **RICH**: Allen Cyn (KU), Randolph 2.3 mi N, Sage Crk Jct 5.1 mi W (A). **SALT LAKE**: Alta, Big Cottonwood Cyn, Butterfield Cyn, City Crk Cyn, Holladay, Lake Blanche, Mill Crk Cyn (C42), Mt Olympus, Red Butte Cyn (U), Salt Lake City (C42). **SAN JUAN**: Abajo Mts (G58), La Sal (C42), Monticello 7.6 mi W (A), Nat Bridges Nat Mon (U). **SANPETE**: Fairview Summit (KU). **SUMMIT**: Mirror Lake 6.4 mi N, Wyoming brdr on U150 (A). **TOOELE**: Clover, Fisher Pass, Tooele (C42). **UINTAH**: Bonanza 25 mi S, Dry Fk rd 13.4 mi N U121 (A), Gusher (C42). **UTAH**: American Fk Cyn, Provo (C42), Silver Lake Flat (A). **WASATCH**: Francis 18.5 mi E, Hanna 14.3 mi W (A). **WASHINGTON**: Kolob (I59), Pine Valley (City), (BAD), Zion Nat Park (C42).

Smith (1979:1435) indicates this as an eastern to northwestern United States species, including Idaho and southern Arizona. It shows a preference for well-shaded woodlands, where it nests under stones and in rotting logs, only occasionally found in the open. Gregg (1963:456) lists it from Colorado between 3500 and 10,400 ft under rocks in a great variety of habitats, predominantly pinyon-juniper and grass. La Rivers (1968:8) lists it from Nevada, where Wheeler and Wheeler (1978:393) found it between 6400 and 9700 ft. They found it in wood and under bark in North Dakota (1963). Cole (1942:374) states that its habitat in Utah is under stones in open and grassy areas, some colonies at 6500 ft. In Utah it nests under stones on rocky, exposed mountain slopes up to 6000 ft (Grundmann 1958:166). Ingham (1959) found it in southern Utah under rocks and logs in oak and aspen.

There were 155 ants in five collections taken from under rocks. In one instance *Tapinoma sessile* was found under the same rock, and once *alienus* was under the same rock with *Formica obscuriventris* and *Lasius niger.* Sixty-nine ants in three collections were taken from under logs. In one case *F. fusca* was under the same log. One ant was taken from a burrow in the open. Four collections were in aspen: one in association with grass, herbs, and conifers and one with fir. Four collections were in sagebrush: two in association with grass and herbs and one with snowberry. One collection was in juniper and pinyon and one in conifers. In 56 recorded Utah habitats it was found 32 times in montane forest. In 32 elevational records it was about equally distributed between 4000 and 9300 ft, slightly more common between 4000 and 6000. Beck et al. (1967:70) found it feeding on dead rodents in one instance in Utah.

Lasius crypticus Wilson

L. crypticus Wilson, 1955, Bull. Mus. Comp. Zool. 113:104; Beck et al. 1967:70; Smith 1979:1436.

Records (Map 15): **BOX ELDER**: Brigham (KU). **CACHE**: Logan (KU). **CARBON**: Myton rd 15 mi E US6 (A). **GARFIELD**: Henry Mts (Wi). **IRON**: Cedar City 14 mi E (A). **KANE**: Long Valley Jct (Wi). **RICH**: Randolph 2.3 mi N (A), Woodruff (BAD). **SAN JUAN**: Geyser Pass, Mexican Water (BAD), Monticello 2 mi W (A). **SANPETE**: Orangeville 19.5 mi W (A). **SEVIER**: Salina Cyn nr Fremont Jct (U). **UINTAH**: Vernal 15 mi N (A). **UTAH**: Provo, Thistle 20.4 mi E (A), Wanrhodes Cyn (KU). **WASATCH**: Hanna 9.2 mi W (A). **WAYNE**: Pleasant Crk (BAD).

Smith (1979:1436) lists this species from midwest to western United States, including Utah and Idaho, nesting under stones or in craters. Cole (1966:20) found its nests under stones in open areas in pinyon-juniper in southern Nevada. Allred and Cole (1971:239) found it in Idaho in a variety of shrub types. Wheeler and Wheeler (1963) found it frequently under rocks, also commonly in soil craters in North Dakota.

Seventy-nine ants in seven collections were taken from under rocks. It was under the same rock with *L. humilis*, and once with *Myrmica americana.* Fifteen ants in one collection were taken from a small crater mound, and 11 in two collections singly in open areas. Five collections were in sagebrush: one in association with grass; one grass, herbs, and rabbitbrush; one herbs and juniper; and one grass, legumes, shrubs, juniper, and pinyon. One collection was in grass, one grass and oak, one pine, and one a cultivated area. In 19 recorded Utah habitats it was taken 9 times in montane forest. Four recorded elevations were between 4307 and 10,750 ft. Beck et al. (1967:70) found it feeding on dead rodents in four instances in Utah.

Lasius fallax Wilson

L. fallax Wilson, 1955, Bull. Mus. Comp. Zool. 113:130; Smith 1979:1437.

Records (Map 15): **CACHE**: Bear River Mts, Logan Cyn (KU). **GRAND**: Warner Ranger Sta (Wi). **SAN JUAN**: Blue Mts (Wi) (? = Abajo Mts). **UINTAH**: Deep Crk (Wi), Red Cloud Loop rd 4.2 mi W U44 (A). **WASATCH**: Soldier Summit 3.3 mi N (A). **COUNTY UNKNOWN**: Bassets Spngs (Uinta Mts) (Wi).

Smith (1979:1437) lists this species from the western United States, including Utah, Colorado, Arizona, Idaho, and Wyoming, nesting under stones in forest clearings.

Fifty ants in two collections were taken from under rocks in sagebrush: one in association with grass and one with matchbrush. Eight collections whose recorded Utah habitats were known were in montane forest. One recorded elevation is 9750 ft.

Lasius humilis Wheeler

L. humilis Wheeler, 1917, Proc. Amer. Acad. Arts, Sci. 52:528.

Records: **IRON**: Cedar City 14 mi E (A). **JUAB**: Ibapah (U). **KANE**: Cedar City 24.3 mi E (A). **UINTAH**: Bonanza (KU).

Smith (1979:1438) lists this species from the western United States, including Colorado and Nevada, nesting under stones in meadows and open woods. Gregg (1963:475) lists it between 5154 and 7000 ft under rocks in meadows in Colorado.

Forty-five ants in two collections were found under logs, one in grass, herbs, aspen, and pine, and one in pine. Ants of *L. subumbratus* were under the same log in one instance, and *L. crypticus* in the other. In two of four recorded Utah habitats it was found in montane forest. Two known elevations are 5288 and 5456 ft.

Lasius nearcticus Wheeler

L. flavus nearcticus Wheeler, 1906, Psyche 13:38; Rees and Grundmann 1940:7; Cole 1942:374; Grundmann 1958:166.

L. flavus claripennis: Cole 1942:375.
L. flavus microps: Ingham 1959:74.

Records (Map 17): **CACHE**: Logan (KU). **DUCHESNE**: Paradise Park 11 mi W (U). **PIUTE**: Fish Lake Jct 1 mi S (U). **SALT LAKE**: Big Cottonwood Cyn (U), Butterfield Cyn (RG), Red Butte Cyn (U). **SAN JUAN**: Bluff, La Sal Mts (RG). **UINTAH**: Bonanza (KU). **WASHINGTON**: Veyo, Zion Nat Park (159).

Smith (1979:1438) lists this species from eastern to western United States, including Colorado and Wyoming, where it nests under rocks or fallen logs in moist woodlands. Hunt and Snelling (1975:22) list it from Arizona. Gregg (1963:471) lists it between 6250 and 9000 ft under rocks in conifers, pinyon-juniper, and oak habitats in Colorado. La Rivers (1968:8) lists it from Nevada, where Wheeler and Wheeler (1978:393) found it between 6200 and 10,400 ft. They found it frequently under rocks in North Dakota (1963). Cole (1942:374) indicates its habitat in Utah as under stones. In Utah it nests under stones or dead wood among cottonwoods (Grundmann 1958:166). Ingham (1959) found it under stones in ash, oak, poplar, and poison ivy in southern Utah.

In 10 recorded Utah habitats it occurred only 4 times in montane forest. In 10 elevation records between 4320 and 8000 ft it occurred 7 times under 5000, twice over 8000.

Lasius niger (Linnaeus)

Formica niger Linnaeus, 1758, Syst. Nat. Ed. 10, 1:580.
L. niger neoniger: Rees and Grundmann 1940:7; Cole 1942:374; Hayward 1945:120; Grundmann 1958:166; Ingham 1959:72.
L. niger: Beck et al. 1967:70; Smith 1979:1436.

Records (Map 16): **BOX ELDER**: Kelton (US), Lucin (BAD), Snowville, Wellsville Mts, Willard Basin (KU). **CACHE**: Ant Valley (KU), Blacksmith Fk Cyn, Cowley Cyn (RG), Franklin Basin (KU), High Crk (US), W. Hodges Cyn (KU), Logan (RG), Logan Cyn, Tony Grove Cyn (KU). **EMERY**: Hideout Cyn nr Green River (U). **GARFIELD**: Escalante 20 mi E (U), Boulder Mt (G58), Osiris, Trachyte Ranch (U). **GRAND**: Moab 12 mi N (U). **KANE**: Coral Pink Sand Dunes (BAD), Kanab 10 mi N (159) and 20 mi N (C42), Zion Nat Park (159). **MILLARD**: Black Rock 8 mi N (KU). **SALT LAKE**: Alta, Big Cottonwood Cyn (RG), Brighton, Butterfield Cyn (U), City Crk Cyn, Lake Blanche (RG), Mt Olympus, Parleys Cyn, Red Butte Cyn (U), Salt Lake City (KU). **SAN JUAN**: Abajo Mts (G58), Blanding 15.6 mi N (A), Bluff (U), Mexican Hat 13 mi S (A), Nat Bridges Nat Mon (Wi), Red Mesa (BAD), White Cyn (Wi). **SANPETE**: Fairview Cyn (KU). **SUMMIT**: Kamas 14.7 mi E (A), Woodland (BAD). **TOOELE**: S Willow Cyn (U). **UINTAH**: Bonanza and 3 mi S (KU), Gusher, Jensen (U), Dry Fk rd 22.8 mi N U121 (A). **UTAH**: American Fk Cyn (C42), Diamond Fk Cyn (KU), Provo Cyn (U), Santaquin Cyn 3.6 and 7.1 mi up, Tibble Fk Cyn, Tibble Fk Lake 0.5 mi W (A), Wanrhodes Cyn (KU). **WASATCH**: Cascade Spngs 3 mi N, Francis 14.4 and 18.5 mi E (A), Fruitland 4 mi W (U), Hanna 14.3 mi W (A), Heber (Wi), Midway, Soapstone Cyn (U), Soldier Summit (US). **WASHINGTON**: Grafton, Kolob, Rockville, Santa Clara Crk, Veyo, Virgin River E Fk (159), Zion Nat Park (WU). **WAYNE**: Elkhorn Ranger Sta, Pleasant Crk (BAD). **WEBER**: Beaver Crk (KU), Ogden (Wi).

Ants that run to *niger* in the key should be considered as "*niger* complex," for some specimens whose records are included here are lighter in color and/or larger than the "typical" *niger*, and may represent a different species.

Smith (1979:1436) lists this species from the western United States, including Utah, Colorado, Arizona, and Idaho, nesting under stones and rotten wood in forests or open situations. Gregg (1963:459) lists it from Colorado between 3500 and 12,400 ft under rocks and logs in a variety of habitats, predominantly conifers. La Rivers (1968:8) lists it from Nevada, where Wheeler and Wheeler (1978:393) found it between 7600 and 9000 ft. They found it frequently in soil craters, and, in North Dakota, also common under rocks (1963). Cole (1942:374) states that in Utah its habitat is under stones and logs at higher elevations to 10,000 ft. Grundmann (1958:166) indicates that in Utah it nests under stones and rotting wood alongside streams between 5000 and 10,000 ft. Ingham (1959, 1963) found it in southern Utah under stones and logs, and in flat craters in open areas in a variety of vegetative types.

There were 188 ants in 13 collections taken from under rocks. *Lasius subumbratus* was under the same rock in two collections, *L. sitiens* in one, and *L. alienus* and *Formica obscuriventris* in one. Six ants in one collection were taken singly in an open area. Eggs were found under one rock in early July, larvae under one in late June, pupae under another in late June, and winged forms under one rock in late July. Eight collections were in aspen: two in association with grass, sagebrush, and snowberry; two maple, oak, and fir; one sagebrush; and one fir. Three collections were in sagebrush: one in association with snowberry and oak, and one with herbs and conifers. One collection was in a grassy meadow with oak and conifers, and one in ephedra and blackbrush. In 79 recorded Utah habitats it occurred 41 times in montane areas. In 51 elevational records between 3500 and 10,000 ft it was somewhat equally distributed between 4000 and 8000, once over 10,000. Beck et al. (1967:70) found it feeding on dead rodents in seven instances in Utah.

When the protective rock is removed, these ants run rapidly into burrows and to the opposite side of the rock. Larvae that are present may be abandoned with no attempt on the part of the workers to carry them into deeper burrows. Sometimes those on the ground stay and work furiously to move the eggs and pupae into the burrows. Under one rock three *Aphaenogaster subterranea* were present that had antennae and legs missing. These likely were captured by *niger.*

Lasius pallitarsis (Provancher)

Formica pallitarsis Provancher, 1881, Nat. Canad. 12:355.

Lasius niger var. *sitkaensis*: Rees and Grundmann 1940:7; Cole 1942:374.

Lasius sitkaensis: Beck et al. 1967:71.

Leptothorax sitkaensis: Knowlton 1975:6.

Records (Map 16): **BOX ELDER**: Snowville (C42). **CACHE**: Bear River Range, Blacksmith Fk Cyn, Franklin Basin, Logan, Logan Cyn (KU). **CARBON**: Scofield (BAD). **DAGGETT**: Red Crk (BAD). **DUCHESNE**: Duchesne 3 mi E (WU). **GARFIELD**: Bryce Cyn Nat Park (WU). **KANE**: Kanab (C42). **RICH**: Meadowville (KU). **SALT LAKE**: Big Cottonwood Cyn, Holladay, Mill Crk Cyn (C42), Red Butte Cyn (U), Salt Lake City (C42). **SAN JUAN**: La Sal (RG), Mexican Hat 13 mi S (A). **SANPETE**: Bluebell Flats (KU), Ephraim 8.8 mi E (A), Mt Pleasant (BAD), Orangeville 27.4 mi W (A). **SEVIER**: Fish Lake (BY), Koosharem (BAD). **UINTAH**: Bonanza (KU), Dry Fk rd 22.8 mi N U121 (A), Gusher (C42), Red Cloud Loop rd 9.2 mi W U44 (A). **UTAH**: Aspen Grove (BAD), Santaquin Cyn 3.6 mi up (A). **WASATCH**: Wallsburg (BAD). **WASHINGTON**: Zion Nat Park (C42). **WAYNE**: Pleasant Crk (BAD).

Smith (1979:1437) lists this species from eastern to western United States, including Arizona and Nevada, nesting under stones or logs in forested areas. Gregg (1963:463) lists it from Colorado between 4600 and 12,200 ft under rocks and logs in a variety of habitats, predominantly conifers. Wheeler and Wheeler (1978:393) found it between 6000 and 9700 ft in Nevada, and frequently under rocks, also common in and under wood and in soil in craters in North Dakota (1963). Cole (1942:374) indicates its habitat in Utah as under stones.

There were 124 ants in six collections taken from under rocks. In one case these ants were under the same rock as *Aphaenogaster subterranea*, and once with *L. subumbratus.* In this latter case the tunnels of the two species of *Lasius* were distinctly apart under separate areas of the boulder. Two ants in one collection were taken singly away from the colony. Three collections were in aspen, one in association with conifers. One collection was in ephedra and blackbrush, one herbs, one a grassy meadow, and one firs. In 34 recorded Utah habitats it was taken 19 times in montane forest. In 15 recorded elevations between 4276 and 8750 ft it was taken most frequently under 6000. Beck et al. (1967:71) found it feeding on dead rodents in eight instances in Utah.

Lasius sitiens Wilson

L. sitiens Wilson, 1955, Bull. Mus. Comp. Zool. 113:108.

Records (Map 17): **CACHE**: Logan (KU). **JUAB**: Fish Spngs Ranch (U), Topaz Mt (KU). **UTAH**: Diamond Fk Cyn (KU), Tibble Fk Cyn (A), Wanrhodes Cyn (KU).

Smith (1979:1437) lists this species from the western United States, including Colorado, Arizona, and Nevada, nesting under stones in dry open areas between 7000 and 8000 ft. Cole (1966:20) found its nests under stones in pinyon-juniper in southern Nevada. Thirty ants in one collection were taken from under a rock in an association of oak, maple, aspen, and fir in Utah.

Lasius subumbratus Viereck

L. umbratus subumbratus Viereck, 1903, Trans. Amer. Ent. Soc. 29:73; Rees and Grundmann 1940:7; Cole 1942:375.

L. subumbratus: Creighton 1950:424.

Records (Map 16): **DUCHESNE**: Mirror Lake (Wi). **GARFIELD**: Bryce Cyn Nat Park (Wi). **GRAND**: Warner Ranger Sta (Wi). **KANE**: Cedar City 24.3 mi E (A), Long Valley Mts (Wi). **SALT LAKE**: Big Cottonwood Cyn, Brighton (U), Lake Blanche (Wi). **SAN JUAN**: Blanding 16.5 mi N (A), Blue Mts (Wi) (? = Abajo Mts). **SANPETE**: Ephraim 8.8 mi E (A). **SUMMIT**: Kamas 4.6 and 9.2 mi E, Mirror Lake 11.6 mi N (A), Shingle Crk (Wi). **UINTAH**: Red Cloud Loop rd 9.2 mi W U44 (A). **UTAH**: Orem (A), Provo (U), Tibble Fk Lake (A), Timpanogos Pk (Wi). **WASATCH**: Cascade Spngs 3 mi N (A). **WEBER**: Woodruff 29.1 mi W (A).

Smith (1979:1439) lists this species from eastern to western United States, including Arizona and Nevada, nesting under stones or logs in meadows and forests. It is a social parasite of *L. pallitarsis*. Gregg (1963:477) lists it from Colorado between 5160 and 9224 ft under rocks and logs in a variety of habitats. Cole (1942:375) indicates it as uncommon in Utah, nesting under stones.

There were 294 ants in nine collections taken from under rocks. In two instances ants of *L. niger* were under the same rocks, and once those of *L. pallitarsus* were present. Ten ants in one collection were found under a log, and 20 ants in one collection singly in a garden. Six collections were taken in conifers: two in association with grass, herbs and aspen; two sagebrush and aspen; one a grassy meadow; and one aspen. Two collections were taken in grass; one sagebrush; one sagebrush, snowberry, and oak; and one a garden. In 22 recorded Utah habitats it was taken 19 times in montane forest. Six recorded elevations were between 5000 and 10,050 ft.

Lasius umbratus (Nylander)

Formica umbrata Nylander, 1846, Acta. Soc. Sci. Fenn. 2:1048.

L. umbratus mixtus var. *aphidicola*: Rees and Grundmann 1940:7; Cole 1942:375.

L. umbratus aphidicola: Ingham 1959:74.

L. umbratus: Smith 1979:1439.

Records (Map 16): **BEAVER**: Beaver 5.5 mi E (U). **CACHE**: Logan Cyn (C42). **IRON**: Cedar City 19 mi E (A). **RICH**: Woodruff (U). **SALT LAKE**: Big Cottonwood Cyn (U), Little Willow Crk Cyn (RG). **SAN JUAN**: Kigalia Ranger Sta (Wi). **SANPETE**: Pine Plantation (KU). **SUMMIT**: Henefer (C42). **UINTAH**: Jensen (U). **UTAH**: Jordan Narrows (C42), Santaquin Cyn 7.1 mi up (A). **WASHINGTON**: Kolob (I59). **WEBER**: Ogden Cyn (C42).

Smith (1979:1439) lists this species from eastern to western United States, including Utah, Arizona, and Idaho, nesting under stones or logs. It is associated with *L. alienus* and *L. niger*. Gregg (1963:478) lists it from Colorado between 5254 and 9500 ft under rocks predominantly in conifer habitats. Wheeler and Wheeler (1963) found it frequently under rocks and in earthen mounds in North Dakota. Cole (1942:375) indicates its habitat in Utah as under stones. Ingham (1959) found it in logs in oak and aspen in southern Utah.

Forty ants in one collection were found under a log, and 40 in another collection under a rock. Two collections were taken in aspen: one in association with pine and one in a grassy meadow. In 14 recorded Utah habitats it was taken 10 times in montane forest. Six recorded elevations were between 4494 and 8402 ft.

Lasius vestitus Wheeler

L. umbratus vestitus Wheeler, 1910, Psyche 17:238.

Record: **SAN JUAN**: La Sal Mts (U).

Smith (1979:1440) lists this species from the western United States, including Idaho. Wheeler and Wheeler (1978:393) found it between 7600 and 8100 ft in Nevada.

Leptothorax ambiguus Emery

L. curvispinosus ambiguus Emery, 1895, Zool. Jahrb. Syst. 8:317.

Records: **BOX ELDER**: Locomotive Spngs (KU). **UTAH**: Spanish Fk Cyn (KU).

Smith (1979:1392) lists this species from midwestern United States; no intermountain state is listed. It nests in soil or hollow grass stems in woodlands and grasslands. Its occurrence in Utah is doubtful.

Leptothorax andrei Emery

L. andrei Emery, 1895, Zool. Jahrb. Syst. 8:318.

Record: **TOOELE**: Granite Mt (U).

Smith (1979:1392) lists this species from western United States, including Arizona and Nevada, nesting under stones. Cole (1966:17) found it in southern Nevada in pinyon-juniper, where it probably nests under stones. Allred and Cole (1971:239) found it in juniper in Idaho.

Leptothorax crassipilis Wheeler

L. acervorum crassipilis Wheeler, 1917, Proc. Amer. Acad. Arts. Sci. Boston 52:513.

L. crassipilis: Creighton 1950:278; Smith 1979:1396.

Record: **CARBON**: Scofield 4 mi S (A).

Smith (1979:1396) lists this species from western United States, including Utah, Colorado, Arizona, and Wyoming, nesting under rocks and logs. Gregg (1963:402) lists it between 5700 and 9100 ft under rocks and logs in conifers, oak, and manzanita habitats in Colorado. La Rivers (1968:6) lists it from Nevada, where Wheeler and Wheeler (1978:391) found it at 8100 ft. Three ants in one collection in Utah were taken from under an aspen log.

Leptothorax furunculus Wheeler

L. furunculus Wheeler, 1909. J. New York Ent. Soc. 17:82; Knowlton 1975:5.

Records: **BOX ELDER**: Cedar Crk (City), Curlew Jct, Hansel Mts, Snowville (K75), Wellsville Mts (KU).

Smith (1979:1393) lists this species from Colorado and Wyoming. Gregg (1963:383) lists it from Colorado between 6970 and 7500 ft in pinyon-juniper areas. Knowlton (1975:5) found it associated with sagebrush in northern Utah.

Leptothorax hirticornis Emery

L. hirticornis Emery, 1895, Zool. Jahrb. Syst. 8:317; Cole 1942:370; Smith 1979:1397.

Record: **SALT LAKE**: locality unknown (C42).

Smith (1979:1397) lists this species from midwest and western United States, including Utah and Colorado, nesting with *Formica obscuripes* in large mounds of detritus in open areas. Gregg (1963:405) lists it between 5354 and 7000 ft in Colorado.

Leptothorax muscorum (Nylander)

Myrmica muscorum Nylander, 1846, Acta Soc. Sci. Fenn. 2:1054.

L. acervorum canadensis: Rees and Grundmann 1940:6; Cole 1942:369; Hayward 1945:120.

L. acervorum canadensis var. *yankee*: Rees and Grundmann 1940:6; Cole 1942:369.

L. canadensis: Ingham 1959:60.

L. muscorum: Beck et al. 1967:71.

Records (Map 17): **BOX ELDER**: Box Elder Cyn (US). **CACHE**: Blacksmith Fk Cyn, W Hodges Cyn (KU), Logan (C42), Logan Cyn Summit, Mendon Cold Spngs (KU), Millville (US), Tony Grove, Wellsville (KU). **GARFIELD**: Osiris (U). **IRON**: Cedar Breaks Nat Mon (I59). **JUAB**: Red Crk Spng (KU). **SALT LAKE**: Big Cottonwood Cyn S Fk (C42), Brighton, Butterfield Cyn (U), Little Cottonwood Cyn (C42). **SANPETE**: Manti (KU). **UINTAH**: Paradise Park (U), Whiterocks Cyn (KU). **UTAH**: American Fk Cyn (U), Aspen Grove (BY), Emerald Lake (BAD).

Smith (1979:1397) lists this species from eastern to western United States, including Arizona, nesting under rocks, logs, or bark of fallen trees in woodlands. Gregg (1963) lists it from Colorado between 5354 and 12,500 ft under rocks and logs in a variety of habitats, predominantly in conifers. La Rivers (1968:6) lists it from Nevada, where Wheeler and Wheeler (1978:391) found it between 6400 and 11,000 ft. Cole (1942:369) indicates its habitat in Utah as under decaying wood and in standing dead trees. Ingham (1959) found it under logs in fir, spruce, and bristlecone pine in southern Utah.

In 22 recorded Utah habitats it was found 15 times in montane forest. In 16 recorded elevations between 4495 and 10,500 ft it was taken most frequently above 7000. Beck et al. (1967:71) found it feeding on dead rodents in one instance in Utah.

Leptothorax nevadensis Wheeler

L. nevadensis Wheeler, 1903, Proc. Acad. Nat. Sci. Phila. 55:224; Rees and Grundmann 1940:6; Cole 1942:370; Knowlton 1970:210, 1975:5.

Records (Map 17): **BEAVER**: Beaver 5.5 mi E (U). **BOX ELDER**: Cedar Crk (City) (K70), Curlew Valley (US), Hansel Mts, Kelton Pass, Snowville (K70). **CACHE**: Blacksmith Fk Cyn (RG), Green Cyn (US). **RICH**: Randolph 8 mi SW (KU). **SANPETE**: Ephraim Cyn (KU).

Creighton (1950) and Smith (1979:1393) list four forms of this species from the western United States, including Nevada, nesting in soil usually under stones. The subspecies that occurs in Utah is likely *rudis* or *nevadensis*. These can be separated by the sculpture on the dorsum of the thorax. On *nevadensis* the thorax is densely and evenly punctate, whereas on *rudis* the punctures are interrupted by prominent rugae on the epinotum and mesonotum. Cole (1966:17) found its nests in southern Nevada in pinyon-juniper and under stones in Utah (1942:370). Wheeler and Wheeler (1978:392) found it between 6100 and 10,000 ft in Nevada. Knowlton (1975:5) found it associated with rabbitbrush and grass in northern Utah. In 10 recorded Utah habitats it was taken four times in montane forest. One recorded elevation is 4544 ft.

Leptothorax nitens Emery

L. nitens Emery, 1895, Zool. Jahrb. Syst. 8:318; Rees and Grundmann 1940:6; Cole 1942:370; Creighton 1950:265; Grundmann 1958:164; Knowlton 1970:211, 1975:6.

Records (Map 18): **BOX ELDER**: Box Elder Cyn (KU), Cedar Crk (City), Hansel Mts (K75), Kelton, Kelton Pass, Snowville (K70) and 13 mi SW, Wellsville Mts (KU). **CACHE**: Providence Cyn (C42), Spring Hollow (US). **GARFIELD**: Boulder Mt (G58). **GRAND**: Moab 10 mi SE (KU). **MILLARD**: Black Rock (US). **SAN JUAN**: Abajo Mts (G58). **UTAH**: American Fk Cyn (RG).

Smith (1979:1394) lists this species from western United States, including Colorado and Wyoming, nesting under rocks and in duff. Hunt and Snelling (1975:22) list it from Arizona. Gregg (1963:384) lists it between 6000 and 8000 ft under rocks in conifers, pinyon-juniper, and oak habitats in Colorado. La Rivers (1968:6) lists it from Nevada, where Wheeler and Wheeler (1978:392) found it at 6300 and 6400 ft. Cole (1942:370) found it under stones in Utah. Grundmann (1958:164) indicates that it nests under stones in desert conditions and transition zones in shrubs in Utah. Knowlton (1975:6) found it associated with horsebrush in northern Utah. In 15 recorded Utah habitats between 4225 and 7000 ft, it was found 7 times in montane areas.

Leptothorax rugatulus Wheeler

L. rugatulus brunnescens Wheeler, 1917, Proc. Amer. Acad. Arts, Sci. 52:510; Creighton 1950:269; Smith 1979:1394.

L. rugatulus: Cole 1942:369; Creighton 1950:268; Grundmann 1958:164; Knowlton 1975:6.

Records (Map 18): **BOX ELDER**: Box Elder Cyn (KU), Cedar Hill (K75), Park Valley (City) (C42), Snowville (K75) and 13 mi SW (KU), Wildcat Hills (K75). **CACHE**: Blacksmith Fk Cyn (US), Green Cyn (KU), Hyde Park (US), Logan Cyn (KU), Richmond (US). **MILLARD**: White Valley (C42). **SALT LAKE**: Red Butte Cyn (U). **SAN JUAN**: Mexican Hat (G58). **SANPETE**: Majors Flats (KU). **TOOELE**: Clover, Delle, Fisher Pass (C42). **UINTAH**: Bonanza 3 mi S (KU). **WEBER**: Uintah (US).

Creighton (1950) and Smith (1979:1394) list two races of this species from the western United States, including Utah and Colorado, where it nests under rocks or wood. The Utah race is likely the subspecies *brunnescens*, which may be separated from *rugatulus* by the thoracic rugae that are well developed on *rugatulus*, but feeble, often replaced by punctures, on *brunnescens*. Hunt and Snelling (1975:23) list it from Arizona. Gregg (1963:387) lists it from Colorado between 5354 and 8700 ft under rocks and logs in a variety of habitats, predominantly conifers. La Rivers (1968:6) lists it from Nevada, where Wheeler and Wheeler (1978:392) found it between 6000 and 10,000 ft. They found it under rocks and other objects in North Dakota (1963). Cole (1942:369) indicates that it nests under stones in Utah. In Utah it occurs in the transition zone (Grundmann 1958:164). Knowlton (1975:6) found it associated with sagebrush and snowberry in northern Utah. In 20 recorded Utah localities it occurred 6 times in montane areas between elevations of 4270 and 6300 ft, mostly at lower elevations.

Leptothorax silvestrii (Santschi)

Tetramorium silvestrii Santschi, 1909, Soc. Ent. Ital., Bol. 41:6.

Record: **BOX ELDER**: Cedar Hill (KU).

Smith (1979:1395) lists this species from southern Arizona nesting in oak above 3500 ft. Its occurrence in Utah is questionable.

Leptothorax tricarinatus Emery

L. tricarinatus Emery, 1895, Arb. Zool. Jahrb. System 8:318; Knowlton 1970:211, 1975:6.

L. tricarinatus tricarinatus: Smith 1952:100; Smith 1979:1395.

L. tricarinatus neomexicanus: Smith 1952:101; Grundmann 1958:164; Ingham 1959:60; Smith 1979:1395.

Records (Map 18): **BOX ELDER**: Kelton (K70). **DUCHESNE**: Avintaquin Cmpgnd (A). **JUAB**: Mt Nebo (US), Nephi 20 mi SW (Sm52). **MILLARD**: White Valley (Sm52). **SANPETE**: Orangeville 19.5 mi W (A). **SUMMIT**: Mirror Lake 17.3 mi N (A). **UINTAH**: Red Cloud Loop rd 19 mi W U44 (A). **WASATCH**: Daniels Pass (US). **WASHINGTON**: Kolob (I59).

Creighton (1950) and Smith (1979:1395) list two races of this species from western United States, including Utah, Colorado, Arizona, and Wyoming, nesting in soil and under rocks in open grassy areas. Both races are known for Utah. The subspecies *neomexicanus* may be separated from *tricarinatus* by the length of the epinotal spines, which are longer on *neomexicanus*, and by the opaque thorax of *neomexicanus* versus the shining surface of *tricarinatus*. Gregg (1963) lists it between 4600 and 7800 ft under rocks in a variety of habitats, predominantly grass areas in Colorado. Grundmann (1958:164) lists it as a plateau form between 6000 and 8000 ft in Utah. Ingham (1959) found it in clumps of dry grass associated with sagebrush, oak, and a variety of herbs in southern Utah.

There were 120 ants in three collections taken from under rocks, and 50 in one collection under a log. Immatures were found under one rock in early July. Two collections were taken in aspen: one in association with fir and one with sagebrush and conifers. One collection was taken in grass and one in pine. It was found in 7 montane areas in 10 localities where the habitat was recorded, at elevations from 4225 to 8000 ft.

Liometopum occidentale Wheeler

L. apiculatum luctuosum Wheeler, 1905, Bull. Amer. Mus. Nat. Hist. 21:325; Rees and Grundmann 1940:6; Cole 1942:371.
L. occidentale luctuosum: Creighton 1950:339; Grundmann 1958:165; Ingham 1959:60.
L. tricarinatus: Knowlton 1970:211, 1975:6.
L. luctuosum: Allred and Cole 1979:99.

Records (Map 18): **CARBON**: Wellington 10 mi NE (A). **DUCHESNE**: Duchesne 9 mi W (WU), Myton (RG). **EMERY**: Greenriver, Gunnison Butte (RG). **GRAND**: Dewey (U), Moab (RG). **KANE**: Glen Cyn City (AC), Kanab 12.5 mi N (A), Mt Carmel Jct, Zion Nat Park (159). **PIUTE**: Marysvale 4.1 mi S (A). **SAN JUAN**: Blanding (G58), Hatch Wash nr La Sal (RG), Monticello 17 mi E (U). **WASHINGTON**: Rockville, Zion Nat Park (159). **WAYNE**: Capitol Reef Nat Park (U).

Creighton (1950) and Smith (1979:1417) indicate two forms of this western United States species, including Colorado, Arizona, and Wyoming. The Utah specimens probably belong to the subspecies *luctuosum* rather than *occidentale*. Gregg (1963:443) lists this species between 4800 and 7550 ft under rocks and logs in conifers and pinyon-juniper in Colorado. Wheeler and Wheeler (1978:392) found it between 5200 and 8100 ft in Nevada. Cole (1966:18) found a nest in southern Nevada in detritus at the base of a juniper; it also nests under stones in Utah, for the most part at elevations above 4000 ft (1942:371). Grundmann (1958:165) indicates this as a mountain species that nests between 4000 and 7000 ft in Utah. Ingham (1959) found it in southern Utah under rocks and bark of living trees in a variety of habitats. Allred and Cole (1979:99) found it in sagebrush-grass and juniper-pinyon associations in southern Utah.

Sixty ants in two collections were taken from small crater mounds, 29 in one collection from under a rock, and 25 in one collection from duff under a pinyon tree. Three collections were taken in sagebrush, one in association with juniper and pinyon. None of 18 recorded Utah localities were in montane areas. In 15 recorded elevations between 3250 and 7300 ft nine are between 4000 and 6000.

Manica hunteri (Wheeler)

Myrmica hunteri Wheeler, 1914, Psyche 21:119.
Manica hunteri: Wheeler and Wheeler 1970:135; Smith 1979:1352.

Record: **CACHE**: Benson (W70).

Smith (1979:1352) lists this species from the western United States, including Utah, Nevada, Idaho, and Wyoming, nesting in open areas of coniferous forests. Wheeler and Wheeler (1970) state that its habitat is under stones in craters in coniferous forest, specifically lodgepole pine, although craters are rare. They found it between 2200 and 9600 ft in Nevada (1978:391).

Manica mutica (Emery)

Myrmica mutica Emery, 1895, Zool. Jahrb. Syst. 8:311; Rees and Grundmann 1940:5; Cole 1942:368.
Manica mutica: Ingham 1959:38; Wheeler and Wheeler 1970:159; Knowlton 1970:211, 1975:6.

Records (Map 19): **BOX ELDER**: Blue Crk (City) (C42), Cedar Hill (K70), Corinne (C42), Kelton, Penrose 7 mi W (KU), Tremonton (C42). **CACHE**: Benson (W70), Hyrum (C42), Lewiston (US). **DAVIS**: NE Antelope Island (W70), Layton (W70), Woods Cross (RG). **GARFIELD**: Osiris, Panguitch (W70). **IRON**: Cedar Breaks Nat Mon (W70), Cedar City (RAU), Coal Crk Cyn (159). **JUAB**: Lexington (US). **KANE**: Long Valley (W70). **MILLARD**: Delta (BY), Fillmore (US). **PIUTE**: Junction (W70). **SALT LAKE**: Big Cottonwood Cyn (U), Great Salt Lake S end, Midvale, Murray (W70), Salt Lake City (RG). **SANPETE**: Chester, Fayette (C42). **TOOELE**: Iosepa, Lake Point, Tooele (C42). **UTAH**: Aspen Grove (BY), Lehi (W70), Provo (U), Salem, Springville (C42), Thistle 14.6 mi E (A), E Utah Lake (BY). **WEBER**: Ogden, Plain City (C42).

Smith (1979:1352) lists this species from midwest and western United States, including Colorado, nesting in a wide variety of habitats, where it is associated with *Formicoxenus chamberlini*. Gregg (1963:316) lists it from Colorado between 4500 and 8600 ft under rocks and wood in conifers, pinyon-juniper, cottonwood-willow, grass, sagebrush, and greasewood habitats. La Rivers (1968:2) lists it from Nevada. Wheeler and Wheeler (1970) list it from Colorado, Arizona, Nevada, Idaho, Wyoming, and Utah, where it often nests in small craterlike mounds in a variety of habitats including coniferous forest, pinyon-juniper, and grasslands between 1100 and 8600 ft. They found it frequently in soil craters in North Dakota (1963). Cole (1942:368) indicates that in Utah it nests under stones and in ditch banks, sometimes constructing small craters. Ingham (1959, 1963) found it under rocks in juniper and alkali flats in southern Utah.

Twenty ants in one collection in Utah were taken from under a rock in an association of grass, clover, Russian thistle, and sagebrush. In 41 recorded habitats it was taken only six times in montane areas. In 35 recorded elevations between 4225 and 10,399 ft it was taken most frequently under 5000, once over 8000.

Monomorium minimum (Buckley)

Myrmica minima Buckley, 1867, Proc. Ent. Soc. Phila. 6:338.

Monomorium minimum: Rees and Grundmann 1940:3; Cole 1942:361; Grundmann 1958:163; Ingham 1959:57; Beck et al. 1967:71; Knowlton 1975:6; Allred and Cole 1979:98.

Records (Map 19): **BEAVER**: Beaver 5.5 mi E (U). **BOX ELDER**: Hansel Mts (K75), Locomotive Spngs (KU). **CACHE**: Ant Valley, Green Cyn, Leeds Cyn (KU). **EMERY**: Huntington (BAD). **GARFIELD**: Boulder (U). **GRAND**: Moab 15 mi S (KU). **IRON**: Highway US91 (I59). **JUAB**: Callao (BAD). **KANE**: Glen Cyn City (AC), W Glen Cyn Res (G58), Grosvenor Arch (US), Kanab (G58) and 20 mi N (C42), Long Valley Jct 2 mi W, Mt Carmel Jct (I59). **MILLARD**: Swasey Spngs (RG). **MORGAN**: Morgan (KU). **SALT LAKE**: Big Cottonwood Cyn (U), Little Willow Cyn (C42), Rose Cyn (U), Salt Lake City (RG). **SAN JUAN**: Blanding (RG), Mexican Hat (G58). **SANPETE**: Manti (KU). **SEVIER**: Sevier (KU). **SUMMIT**: Echo (BAD). **TOOELE**: Clover, Fisher Pass, Little Valley Ranger Sta, Orrs Ranch (C42). **UTAH**: American Fk (RG), Aspen Grove (BY), Diamond Fk Cyn, Spanish Fk Cyn (KU). **WASATCH**: Provo River N Fk (U). **WASHINGTON**: Highway 18 (I59), Pinto 3 mi S (US) and 3 mi N (KU), Zion Nat Park (I59). **WEBER**: Hooper (C42).

Smith (1979:1382) lists this species from Canada to Florida and western United States, including Colorado, with nests in exposed soil, under objects, or in rotting wood. Hunt and Snelling (1975:21) list it from Arizona. Gregg (1963:368) lists it between 3500 and 8500 ft under rocks predominantly in pinyon-juniper areas in Colorado. Cole (1966:16) found it in southern Nevada under stones in blackbrush and other desert shrub types, rarely in pinyon-juniper. He states that in Utah it nests under stones, in crater mounds, under bark, or in logs (1942:361). Allred and Cole (1979:98, 1971:239) found it in southern Utah and Idaho in a variety of desert shrub types. Wheeler and Wheeler (1963) found it commonly in soil craters in North Dakota. Grundmann (1958:163) found it abundant in transition zones and canyon sides under stones in Utah. Ingham (1959, 1963) found it under stones or in small crater mounds in open areas associated with sagebrush, juniper, thistlepoppy, galletagrass, little rabbitbrush, winterfat, and greasewood in southern Utah. Knowlton (1975:6) found it associated with rabbitbrush in northern Utah.

In 43 recorded Utah habitats only 10 were in montane areas. Twenty-seven elevational records between 3250 and 8000 ft show it most common (24 times) between 4000 and 7000. Beck et al. (1967:71) found it feeding on dead rodents in three instances in Utah.

Myrmecocystus flaviceps Wheeler

M. yuma var. *flaviceps* Wheeler, 1912, Psyche 19:174.

M. flaviceps: Snelling 1976:85; Smith 1979:1446.

Records (Map 19): **JUAB**: Callao 5 mi E (U). **MILLARD**: Black Rock (US) and 5 to 8 mi N, Deseret 30 to 32 mi S (S76). **WASHINGTON**: Harrisburg (S76), Zion Nat Park (WU).

Smith (1979:1446) lists this species from western United States, including Utah, Arizona, and Nevada. Snelling (1976:85) indicates that its nests are craterlike in juniper, sagebrush, saltbush-greasewood, creosote bush, creosote bush-bur sage, and palo verde-cactus.

Myrmecocystus hammettensis Cole

M. hammettensis Cole, 1938, Amer. Midl. Natl. 19:678.

Record: **BOX ELDER**: Park Valley (City) 31 mi SW (KU).

Smith (1979:1446) lists this species from western United States, including Nevada and Idaho. Snelling (1976:102) indicates its habitat as saltbush-greasewood and sagebrush-grass in craterlike nests.

Myrmecocystus kennedyi Cole

M. melliger semirufus var. *kennedyi* Cole, 1936, Ent. News 47:119.

M. melliger semirufus: Cole 1942:386.

M. kennedyi: Creighton 1950:449; Grundmann 1958:167; Snelling 1976:65; Smith 1979:1446.

Records: **BOX ELDER**: Lucin (C42). **GRAND**: Moab (C42). **JUAB**: Silver City (US). **WASHINGTON**: St George 5 mi S (S76).

Smith (1979:1446) lists this species from western United States, including Utah, Arizona, Nevada, and Idaho. Snelling (1976:66) lists its habitats as sagebrush, creosote bush-bur sage, and palo verde-cactus, where nests occur as craters in bare areas away from vegetation. Cole (1942:386) indicates its habitat as craterlike nests in open areas in Utah. None of four recorded Utah habitats were in montane areas. Four recorded elevations were between 4000 and 6100 ft.

Myrmecocystus mendax Wheeler

M. melliger mendax Wheeler, 1908, Bull. Amer. Mus. Nat. Hist. 24:351; Rees and Grundmann 1940:11; Cole 1942:385.

M. melliger: Allred and Cole 1979:98.

Records: **CACHE**: Wellsville (RG). **EMERY**: Greenriver (US). **KANE**: Glen Cyn City (AC). **MILLARD**: Swasey Spngs (C42). **SAN JUAN**: Dead Horse Pt State Park (US).

Smith (1979:1447) lists this species from western United States, including Colorado, Arizona, and Nevada. Gregg (1963:645) lists it between 3600 and 6600 ft under rocks and in crater nests in pinyon-juniper and grass habitats in Colorado. Snelling (1976:40) indicates its habitats as pinyon-oak, mesquite-acacia, pinyon-juniper, oak-juniper, and shrubs between 3600 and 6600 ft. Cole (1942:386) indicates that in Utah its nests are in unprotected soil of open areas. Allred and Cole (1979:98) found it in a variety of desert shrub types in southern Utah with no apparent plant preference. None of the recorded habitats in Utah were from montane areas, and four recorded elevations were between 3250 and 6000 ft.

Myrmecocystus mexicanus Waesmael

M. mexicanus Wesmael, 1838, Bull. Acad. Sci. Belg. 5:770; Garrett 1910:342; Snelling 1976:122; Allred and Cole 1979:98; Smith 1979:1447.

M. mexicanus hortideorum: Rees and Grundmann 1940:11; Cole 1942:386; Creighton 1950:446; Grundmann 1958:166; Ingham 1959:75; Beck et al. 1967:71.

Records (Map 20): **EMERY**: Green River, Gunnison Butte (RG). **GARFIELD**: Boulder, Henry Mts (S76), Shootering Cyn (US). **GRAND**: Arches Nat Park (S76), Moab (G58), Thompson (C42). **IRON**: Shirts Cyn (RAU). **KANE**: Glen Cyn City (AC). **MILLARD**: Black Rock (US) and 5 mi N (KU), Deseret 32 mi S (S76). **SALT LAKE**: Garfield (S76). **SAN JUAN**: Aztec Cyn (U), Blanding (G58), Bluff (RG), Four Corners, Mexican Water, Montezuma Crk, Red Mesa (BAD). **WASHINGTON**: Hurricane 3 mi SW (159), Pine Valley (City) (BAD), Santa Clara (US), St George (BY).

Smith (1979:1447) lists this as a western species of United States, including Utah, Colorado, Arizona, and Nevada. Gregg (1963:648) lists it between 4500 and 6800 ft in large craters predominantly in pinyon-juniper and sagebrush habitats in Colorado. In southern Nevada Cole (1966) found it abundantly in hopsage-matrimony vine, Russian thistle, blackbrush, and pinyon-juniper habitats. It was scarce in creosote bush areas. Nests in Utah are craterlike, generally on hills and ridges with sparse cover (Cole 1942:386). Grundmann (1958:166) indicates it as a desert species in Utah that occasionally may be found chewing on the ears of mice caught in traps. Ingham (1959, 1963) found it in southern Utah in a variety of shrub types, and Allred and Cole (1979:98, 1971:239) found it in southern Utah and Idaho in a variety of desert shrub types. Snelling (1976:124) indicates that its nests are craterlike.

In 31 recorded Utah habitats it was never found in a montane area. In 18 elevational records it was about equally distributed between 2625 and 6675 ft, slightly more common above 4000. Beck et al. (1967:71) found it feeding on dead rodents in 13 instances in Utah.

Myrmecocystus mimicus Wheeler

M. melliger mimicus Wheeler, 1908, Amer. Mus. Nat. Hist., Bull. 24:353.

M. mimicus: Ingham 1959:76; Allred and Cole 1979:99.

Records: **CACHE**: Green Cyn (KU). **WASHINGTON**: Grafton, Harrisburg Jct 2 mi W, Harrisburg Jct toward Hurricane (159).

Smith (1979:1447) lists this species from midwest to western United States, including Arizona. Cole (1966:22) found it commonly in creosote bush habitats in southern Nevada, as well as some other desert shrub types. The nests are holes in the ground or in craters in open areas. Ingham (1959, 1963) found it in southern Utah in craters in bur sage, rabbitbrush, cholla, creosote bush, mesquite, sagebrush, joshua trees, sand sage, four-wing saltbush, and shadscale. Allred and Cole (1979:99) found it in juniper-ephedra-grass, ephedra-grass, and blackbrush associations in southern Utah. Snelling (1976:58) lists pinyon-juniper, oak-juniper, sagebrush, saltbush-greasewood, creosote bush-bur sage, and grassland at habitats below 4000 ft. Nests are craterlike, frequently concealed by a grass clump. Only one of four recorded Utah habitats was in a montane area. Five recorded elevations were between 2700 and 5000 ft. Snelling (pers. comm.) believes that these Utah records are misidentifications.

Myrmecocystus navajo Wheeler

M. mexicanus navajo Wheeler, 1908, Bull. Amer. Mus. Nat. Hist. 24:360; Cole 1942:386.

M. navajo: Grundmann 1958:167; Snelling 1976:126; Smith 1979:1447.

Records: **BEAVER**: Milford 26.7 mi W (A). **JUAB**: Trout Crk (City) 9 mi E (S76). **MILLARD**: Delta 60 mi W (S76), White Valley (C42). **SAN JUAN**: Bluff (G58).

Smith (1979:1447) indicates this as a western United States species, including Utah, Colorado, Arizona, and Nevada. Gregg (1963:651) lists it between 4100 and 4400 ft in craters in grass habitats in Colorado. Cole (1942:386) indicates that in Utah the nests are inconspicuous in open areas. Grundmann (1958:167) states that in Utah it inhabits obscure ground burrows, with the sand spread out in the form of a disc. Snelling (1976:128) indicates that nests are in the center of a flat disc or may be craterlike in saltbush-greasewood. Fifty ants in one collection were taken from a crater mound in shadscale in Utah.

Myrmecocystus pyramicus Smith

M. pyramicus Smith, 1951, Great Basin Nat. 11:91; Beck et al. 1967:71.

Record: **SAN JUAN**: Mexican Water (BAD).

Smith (1979:1447) lists this species from western United States, including Nevada and Idaho. Snelling (1976:135) indicates its habitats as sagebrush and saltbush-greasewood, with craterlike nests between 2350 and 6700 ft. Beck et al. (1967:71) found it feeding on dead rodents in two instances in Utah.

Myrmecocystus romainei Cole

M. melliger semirufus var. *romainei* Cole, 1936, Ent. News 47:120.

M. romainei: Snelling 1976:81; Smith 1979:1447.

Records (Map 20): **BOX ELDER**: Park Valley (KU). **EMERY**: Greenriver (S76). **GARFIELD**: Dixie State Park (S76). **IRON**: Beryl (S76). **KANE**: Glen Cyn City (AC). **MILLARD**: Delta, Lynndyl (S76). **SAN JUAN**: Bluff (S76). **UINTAH**: Dinosaur Nat Mon, Jensen (S76). **WASHINGTON**: Enterprise, Leeds (S76).

Smith (1979:1447) lists this species from midwest to western United States, including Utah, Colorado, Arizona, and Nevada. Snelling (1976:81) designates its habitats as grass, pinyon-juniper, and creosote bush-tarbush in irregular crater nests. None of 12 recorded Utah habitats were in montane areas. In 11 recorded elevations between 2750 and 5600 ft, 9 were above 4000.

Myrmecocystus semirufus Emery

M. melliger var. *semirufus* Emery, 1893, Zool. Jahrb. Syst. 7:667.

M. semirufus: Grundmann 1958:167; Gregg 1963:653.

Records: **BOX ELDER**: Park Valley (City) 31 mi SW (KU). **DUCHESNE**: Dinosaur Nat Mon (Gr63).

Smith (1979:1448) lists this species as extreme western United States, but does not list an intermountain state. Snelling (pers. comm.) believes these Utah records to be misidentifications of *M. kennedyi*, *M. mendax*, or *M. romainei*. Gregg (1963:653) lists *semirufus* from Colorado between 4800 and 5000 ft under rocks and in crater nests in pinyon-juniper and cottonwood-willow habitats, and gives a record for Utah. La Rivers (1968:9) lists it from Nevada. Grundmann (1958:167) states that in Utah it lives in ground burrows surrounded by a sand crater. Snelling (1976:49) indicates its habitats as oakwoods, pinyon-juniper, sagebrush, creosote bush-bur sage, and creosote bush, with craterlike nests at elevations between 4000 and 5000 ft.

Myrmecocystus testaceus Emery

M. melliger var. *testaceus* Emery, 1893, Zool. Jahrb. Syst. 7:667.

M. testaceus: Beck et al. 1967:71; Snelling 1976:138; Smith 1979:1448.

M. mojave: Beck et al. 1967:71.

Records: **BEAVER**: Minersville (BAD). **BOX ELDER**: Lucin (BAD). **CARBON**: Price (BAD). **EMERY**: San Rafael River (BAD). **JUAB**: Callao (BAD). **KANE**: Adairville (BAD). **MILLARD**: Swasey Spngs (S76). **SAN JUAN**: Four Corners, Mexican Water, Montezuma Crk, Red Mesa (BAD). **UINTAH**: Duchesne 3 mi E (S76). **WASHINGTON**: Pine Valley (City) (BAD). **WAYNE**: Pleasant Crk (BAD).

Smith (1979:1448) lists this species from western United States, including Utah, Nevada, and Idaho. Snelling (1976:139) indicates its habitats as sagebrush, pinyon-juniper, and chaparral between 1400 and 6900 ft in craterlike mounds. Four known specific habitats in Utah were in desert areas under 6000 ft.

Myrmica americana Weber

M. sabuleti americana Weber, Lloydia 2:144; Rees and Grundmann 1940:5; Cole 1942:368.

M. americana: Creighton 1950:94; Grundmann 1958:162; Ingham 1959:36; Knowlton 1975:6; Smith 1979:1348.

Records (Map 20): **BOX ELDER**: Cedar Hill (US), Hansel Mts, Kelton Pass (K75), Wildcat Hills (US). **CACHE**: Logan Cyn Summit (KU). **GARFIELD**: Bryce Cyn Nat Park (C42). **KANE**: Long Valley Jct 2 mi W (159). **RICH**: Randolph 2.3 mi N, Sage Crk Jct 5.1 mi W (A). **SALT LAKE**: Big Cottonwood Cyn, Butterfield Cyn (U). **SAN JUAN**: Abajo Mts (G58). **SANPETE**: Orangeville 19.5 mi W (A). **SUMMIT**: Kamas 21 and 26.4 mi E, Wyoming brdr on U150 (A). **UINTAH**: Bonanza 25 mi S (A).

Smith (1979:1348) designates this as a common grassland species more common east of the Rocky Mountains and rare in the west, but known from Utah, Colorado, and Arizona. Gregg (1963:310) lists it between 3500 and 7500 ft under rocks and wood in conifers, pinyon-juniper, oak, mahogany, and grassy areas in Colorado. La Rivers (1968:2) lists it from Nevada. Wheeler and Wheeler (1978:389) found it at elevations as high as 10,400 ft in Nevada, and commonly under rocks in North Dakota (1963). Cole (1942:368) indicates that in Utah it nests under stones. Grundmann (1958:162) designates it as a mountain form from oak-juniper to aspen-fir, nesting under stones in Utah. Ingham (1959) found it under stones in southern Utah. Knowlton (1975:6) found it associated with rabbitbrush in northern Utah.

Fifty-five ants in three collections in Utah were taken from under rocks, one under the same rock with *Lasius crypticus*. One collection was in conifers, one grass, and one juniper and pinyon. In 17 localities 9 were in canyon-montane forest habitats. Five recorded elevations were between 6500 and 7977 ft.

Myrmica brevispinosa Wheeler

M. rubra brevinodis var. *brevispinosa* Wheeler, 1907, Bull. Wis. Nat. Hist. Soc. 5:74.

M. brevinodis discontinua: Beck et al. 1967:71.

Records (Map 20): **CARBON**: Price (U), Scofield (BAD). **EMERY**: Carter Crk nr Green River (U). **RICH**: Laketown (BAD), Woodruff 13.8 and 18.4 mi W (A). **SAN JUAN**: Abajo Mts (U). **TOOELE**: Blue Lakes (30 mi S Wendover), Gold Hill (U). **UINTAH**: Ashley Crk nr Vernal, Paradise Park 11 mi S (U). **WASHINGTON**: Pine Valley (BAD).

Creighton (1950) and Smith (1979:1348) list two races of this species from midwest to western United States, including Colorado, Idaho, and Wyoming, nesting near streams or permanent bodies of water. The Utah race is likely *discontinua*, which may be distinguished by its dark brown color in contrast to the orange yellow color of *brevispinosa*. Gregg (1963:299) lists this species between 4600 and 10,850 ft under rocks and wood in conifers, pinyon-juniper, and cottonwood-willow habitats in Colorado. Wheeler and Wheeler (1963) found it under rocks in North Dakota.

Eighty ants in one collection were taken from under a rock, and one ant from under a log where *Formica gnava* was present. Two collections were in aspen, one in association with grass, sagebrush, and conifers. In 12 recorded Utah habitats 4 were in montane forest. Nine recorded elevations were between 5566 and 8000 ft. Beck et al. (1967:71) found it feeding on dead rodents in three instances in Utah.

Myrmica emeryana Wheeler

M. scabrinodis schenki var. *emeryana* Wheeler, 1917, Proc. Amer. Acad. Sci. Arts 52:504.

M. scabrinodis sulcinodoides: Rees and Grundmann 1940:5.

M. scabrinodis brevinodis: Rees and Grundmann 1940:5.

M. schenecki emeryana: Cole 1942:368.

M. scabrinodis mexicana: Cole 1942:368.

M. emeryana tahoensis: Creighton 1950:99; Smith 1979:1349.

M. emeryana emeryana: Grundmann 1958:161.

M. emeryana: Ingham 1959:36.

Records (Map 21): **BEAVER**: Beaver 5.5 mi E (U). **CACHE**: Franklin Basin, Leeds Cyn, Logan Cyn, Tony Grove Cyn (KU). **GARFIELD**: Aquarius Plateau (G58), Boulder (U), Bryce Cyn Nat Park (RG), Escalante 20 mi E (U). **KANE**: Long Valley Jct 11 mi W (159). **SALT LAKE**: Big Cottonwood Cyn, Butterfield Cyn (U). **SAN JUAN**: Abajo Mts (U). **SUMMIT**: Soapstone Ranger Sta (U). **UINTAH**: Ashley Crk nr Vernal (U). **UTAH**: Aspen Grove (BY), Halls Fk rd 5.2 mi N Hobble Crk rd (A), Leki (? = Lehi) (C42), Mt Timpanogos (BY).

Creighton (1950) and Smith (1979) designate two races of this species occurring at high elevations in the mountains of western United States, including Utah, Arizona, Nevada, and Wyoming. The subspecies *tahoensis* may be separated from *emeryana* by the lamina of the antennal scape, which is small and diagonally transverse on *emeryana*, but is a prominent median flange on *tahoensis*. Gregg (1963:312) lists this species from Colorado between 5800 and 9713 ft under rocks in conifers, oak, manzanita, and pinyon-juniper areas. Cole (1966:3) states that in southern Nevada it is found under stones in pinyon-juniper. Wheeler and Wheeler (1978:389) found it at 9000 and 10,400 ft in Nevada and commonly in wood and under rocks in North Dakota (1963). Grundmann (1958:161) states that it is a mountain form in Utah, generally associated with aspen-fir above 5000 ft, and making nests under stones. Ingham (1959) found it under stones in grass in southern Utah.

One ant was collected under a rock in a meadow of grass, sedges, and herbs. Other ants under the same rock were *Formica fusca, F. gnava*, and *Myrmica monticola*. In 18 of 19 collections in Utah it was taken in canyon-montane forest. The 12 recorded elevations varied between 4562 and 8000 ft, 9 above 7000.

Myrmica hamulata Weber

M. sabuleti hamulata Weber, 1939, Lloydia 2:146.
M. hamulata: Creighton 1950:99.
M. hamulata hamulata: Smith 1979:1349.

Record: **GARFIELD**: Rubys Inn (US).

Creighton (1950) and Smith (1979:1349) list two forms of this species from midwest and western United States, including Utah, Colorado, and Arizona, nesting in upland plateaus between 7000 and 8000 ft. The Utah form is likely *hamulata*. Gregg (1963:300) lists this species between 8000 and 8700 ft in conifers, oak, and manzanita in Colorado.

Myrmica incompleta Provancher

M. incompleta Provancher, 1881, Nat. Canad. 12:359; Smith 1979:1349.
M. rubra brevinodis var. *sulcinodoides*: Rees and Grundmann 1940:5.
M. rubra brevinodis: Rees and Grundmann 1940:5.
M. brevinodis sulcinodoides: Cole 1942:368.
M. brevinodis: Cole 1942:368; Creighton 1950:95; Ingham 1959:36; Knowlton 1970:211, 1975:6.
M. incompleta incompleta: Smith 1979:1349.

Records (Map 21): **BOX ELDER**: Kelton (K75) and 6 mi N (K70), Tremonton (KU). **CACHE**: Blacksmith Fk Cyn, Elk Valley, W Hodges Cyn (KU), Logan (C42), Logan Cyn (KU), Riverheights (RG), Tony Grove Cyn (KU). **CARBON**: Scofield (BAD). **RICH**: Garden City (KU), Laketown (BAD), Pickleville (KU). **SALT LAKE**: Big Cottonwood Cyn, Salt Lake City (RG). **SUMMIT**: Woodland (C42). **UINTAH**: Ashley Crk nr Vernal (U). **UTAH**: Provo (BY). **WASATCH**: Deer Crk Res, Heber (U). **WASHINGTON**: Pine Valley (City) (BAD). **WAYNE**: Bicknell (U). **WEBER**: Beaver Crk head of, Monte Cristo 8 mi S, Roy 2 mi S (KU). **COUNTY UNKNOWN**: Beaver Head (KU).

Creighton (1950, as *M. brevinodis*) and Smith (1979:1349) list two races of this species, only one occurring in eastern to western United States, including Utah and Colorado, nesting under various objects through a wide elevational range. The Utah subspecies is likely *sulcinodoides*. Hunt and Snelling (1975:21) list this species from Arizona. Gregg (1963) lists it between 4600 and 10,500 ft under logs and rocks in juniper, mahogany, coniferous forest, grass, and other areas in Colorado. La Rivers (1968:2) lists it from Nevada, where Wheeler and Wheeler (1978:389) found it between 6400 and 9700 ft. Cole (1942:368) indicates its habitat in Utah as under stones, and Ingham (1959) found it under stones in southern Utah.

In 27 recorded Utah localities it was found 11 times in montane areas. In 19 recorded elevations it was about equally distributed between 4225 and 7675 ft.

Myrmica lobicornis Emery

M. rubra scabrinodis var. *fracticornis* Emery, 1895, Zool. Jahrb. Syst. 8:313.
M. scabrinodis lobocornis var. *fracticornis*: Rees and Grundmann 1940:5.
M. lobicornis fracticornis: Cole 1942:368; Beck et al. 1967:71; Smith 1979:1349.
M. lobicornis lobifrons: Creighton 1950:100; Ingham 1959:37; Knowlton 1975:6; Smith 1979:1350.
M. lobifrons: Knowlton 1970:211.

Records (Map 21): **BOX ELDER**: Snowville (K70). **CACHE**: Franklin Basin, Logan Cyn summit, Tony Grove Cyn (KU). **DAGGETT**: Radosovich Ranch (BAD). **DUCHESNE**: Fruitland (U), Neola (C42). **GARFIELD**: Boulder Mt (U). **IRON**: Cedar Breaks Nat Mon (I59). **KANE**: Adairville (BAD), Long Valley Jct 11 mi W (I59). **RICH**: Laketown (BAD). **SALT LAKE**: Alta, Big Cottonwood Cyn S fk (C42), Brighton, Butterfield Cyn, Red Butte Cyn (U). **SANPETE**: Bluebell Flats, Ephraim Cyn (KU), Wales (RG). **SUMMIT**: Camas (? = Kamas) (C42) and 21 mi E (A), Henrys Fk Basin (RG), Soapstone Cyn (RG). **TOOELE**: S Willow Cyn (U). **UINTAH**: Whiterocks Cyn (KU). **UTAH**: American Fk Cyn (U), Colton (BAD). **WASATCH**: Currant Crk (BAD), Deer Crk Res. (U). **WASHINGTON**: Pine Valley (City) (BAD).

Creighton (1950) and Smith (1979) list two subspecies from eastern to western United States, including Utah, Colorado, and Arizona, nesting under stones or wood near streams, where they are associated with *Leptothorax provancheri.* Records of both are reported from Utah. They may be separated by the antennal lamina, which encircles the bend of the scape in the form of a saucerlike flange on *lobifrons* but forms an angular toothlike projection on the inner side of the bend on *fracticornis.* Gregg (1963:303) lists this species between 6240 and 12,500 ft under rocks and logs in conifers, oak, manzanita, birch, pinyon-juniper, sagebrush, and mahogany habitats in Colorado. La Rivers (1968:2) lists it from Nevada, where Wheeler and Wheeler (1978:389) found it between 6400 and 10,800 ft. They found it frequently in wood, and also commonly under rocks in North Dakota (1963). Allred and Cole (1971:239) found it in Idaho in association with a variety of shrub types. Cole (1942:368) indicates that it nests under stones and in logs in Utah. Ingham (1959) found it under stones or wood in coniferous forests in southern Utah. Knowlton (1975:6) found it associated with rabbitbrush in northern Utah.

Twenty ants in one collection were taken from under a rock in conifers. In 31 reported Utah habitats it was taken 21 times from montane areas. In 19 recorded elevations between 4544 and 10,500 ft it was about equally distributed, taken once under 5000 and three times over 9000. Beck et al. (1967:71) found it feeding on dead rodents in six instances in Utah.

Myrmica monticola Wheeler

M. scabrinodis schenki var. *monticola* Wheeler, 1917, Proc. Amer. Acad. Arts Sci. Boston 52:505.

M. scabrinodis: Hayward 1945:120.

M. monticola: Knowlton 1970:211, 1975:7.

Records (Map 21): **BOX ELDER**: Cedar Crk (City) (K70), Cedar Hill (K75), Curlew Valley (KU), Hardup (K75), Kelton, Kelton Pass, Snowville (K70), Wildcat Hills (K75). **GRAND**: Moab 10 mi SE (KU). **SAN JUAN**: Pack Crk (US). **SANPETE**: Majors Flat (KU). **UTAH**: Halls Fk rd 5.2 mi N Hobble Crk rd (A). **COUNTY UNKNOWN**: locality given as "Mt Timpanogos or Uinta Mts" (H).

Smith (1979:1350) lists this species from eastern to western United States, including Colorado, nesting under objects in woodlands. Gregg (1963:309) lists it between 6000 and 8600 ft under rocks and logs in conifers, oak, pinyon-juniper, birch, and grass habitats in Colorado. Wheeler and Wheeler (1963) found it frequently in and under wood in North Dakota. Knowlton (1975:7) found it associated with sagebrush, grass, and junipers in northern Utah.

One ant was collected from under a rock in a meadow association of grass, herbs, and sagebrush. Other ants under the same rock were *M. emeryana*, *Formica fusca*, and *F. gnava.* In 13 recorded Utah habitats it was taken only twice in montane forest. Two recorded elevations were 4225 and 4544 ft.

Neivamyrmx californicus (Mayr)

Eciton californicum: Mayr, 1870, Verh. Zool.-Bot. Ges. 20:969.

Eciton sp.: Cole 1942:360; Ingham 1963:40.

N. californicus: Smith 1979:1330.

Records: "MILFORD CO" (C42) (? = Milford in Beaver Co). **IRON**: Modena (I63).

Smith (1979:1330) lists this species from western United States, including Utah and Nevada. Ingham (1963) found it in sagebrush in southern Utah. One recorded elevation in Utah was 5468 ft.

Paratrechina parvula (Mayr)

Prenolepis parvula Mayr, 1870, Zool.-Bot. Ges. Wien, Verh. 20:947.

Paratrechina sp.: Beck et al. 1967:72.

Paratrechina parvula: Smith 1979:1444.

Records: **DUCHESNE**: Tabiona 11.6 mi E (A). **SAN JUAN**: Four Corners, Mexican Water (BAD).

This is tentatively listed as *parvula.* Smith (1979:1444) lists it from eastern to western United States, including Utah and Arizona, nesting under stones and logs or in small craters in open grassy areas.

Sixteen ants in one collection in Utah were taken from under a rock in sagebrush. Beck et al. (1967:72) found it feeding on dead rodents in two instances in Utah.

Pheidole bicarinata Forel

P. bicarinata race *vinelandica* Forel, 1886, Ann. Soc. Ent. Belg. 30:45; Ingham 1963:78.

P. bicarinata buccalis: Creighton 1950:171; Grundmann 1958:163.

P. bicarinata: Ingham 1959:50; Beck et al. 1967:72.

P. longula: Ingham 1963:77.

P. bicarinata paiute: Allred and Cole 1979:98.

P. bicarinata vinelandica: Smith 1979:1367.

Records (Map 22): **BEAVER**: Frisco (BAD). **BOX ELDER**: Lucin (BAD). **CARBON**: Wellington 10 mi NE (A). **DUCHESNE**: Roosevelt (BAD). **GRAND**: Dewey

Bridge, Moab (G58). **KANE**: Adairville, Cottonwood Crk (BAD), Glen Cyn City (AC), Navajo Wells (BAD). **MILLARD**: Desert Range Exp Sta (BAD). **SAN JUAN**: Abajo Mts (U), Four Corners (BAD), La Sal Jct 1.6 and 23.1 mi S (A), Montezuma Crk (BAD). **UINTAH**: Jensen (BAD). **WASHINGTON**: Diamond Valley, Grafton (BAD), Pintura (I59), Rockville, nr Short Crk (Arizona) (BAD), Snow Cyn (I63), Springdale (I59), Timpoweap Cyn (I63), Toquerville (BAD), Zion Nat Park (I59).

Creighton (1950) and Smith (1979) list four races of this species primarily as eastern and central United States, occurring in Colorado, Utah, Arizona, Nevada, and Wyoming, nesting in logs, exposed soil, or under objects in grassy areas. The subspecies may be separated by the following key.

1. Basal face of epinotum in the major largely covered with transverse striae .... *bicarinata*

— Basal face of epinotum in the major largely punctate 2

2(1). Epinotum of minor with angular teeth, broad at the base and not resembling spines .... *longula*

— Epinotum with thick, short spines 3

3(2). Color of major reddish to blackish brown, minor dull yellow to blackish brown .... *paiute*

— Color of major clear yellow to yellowish brown, minor clear yellow .... *vinelandica*

Gregg (1963:408) lists it in Colorado between 3500 and 6970 ft under rocks and logs in a variety of habitats. Cole (1966:15) found it in southern Nevada under stones in various types of desert brush. Wheeler and Wheeler (1963) found it about equally under rocks and wood in North Dakota. Ingham (1959, 1963) found it in southern Utah under stones or in roots of oak and rabbitbrush, or in craterlike mounds in open areas in a variety of vegetative types. Allred and Cole (1979:99) found it in southern Utah in a wide variety of desert shrub types, abundantly in sagebrush.

Twenty ants in one collection were taken from a small mound, 50 in one collection from under a rock, and one singly in an open area. Three collections were taken in sagebrush: one in association with grass, one pinyon, and one juniper and pinyon. Only one of 27 localities in Utah was in a montane forest. Of 23 recorded elevations between 2500 and 7500 ft, 20 were between 3000 and 6000. Beck et al. (1967:72) found it feeding on dead rodents in 19 instances in Utah.

Pheidole californica Mayr

P. californica Mayr, 1870, Verh. Zool. Bot. Ges. Wien 20:987; Rees and Grundmann 1940:4; Cole 1942:362; Grundmann 1958:163.

P. californica oregonica: Cole 1942:362; Ingham 1959:52.

Records (Map 22): **GRAND**: Moab (C42). **KANE**: Kanab (C42). **SALT LAKE**: Big Cottonwood Cyn (U), Ft Douglas (C42), Mt Olympus (U), Salt Lake City (RG). **SAN JUAN**: Abajo Mts (G58), La Sal (C42). **TOOELE**: Clover, Fisher Pass (C42). **UTAH**: Ironton (C42).

Creighton (1950) lists five and Smith (1979:1368) three races of this species from western United States, including Idaho, Arizona, and Nevada. The two races recorded for Utah may be separated by the occipital rugae of the major, which are coarse and wavy on *californica* and fine and essentially straight on *oregonica*. Cole (1942:362) indicates the habitat of this species in Utah as under stones in dry grassy areas. Grundmann (1958:163) indicates that in Utah it nests under stones or in soil around roots, generally in grass habitats. Ingham (1959, 1963: found it in dry sandy soil in sagebrush in southern Utah. Only 3 of 11 localities in Utah were in montane forest. Twelve recorded elevations ranged from 4042 to 7125 ft, 11 under 6000.

Pheidole ceres Wheeler

P. ceres Wheeler, 1904, Bull. Amer. Mus. Nat. Hist. 20:10; Grundmann 1958:163; Beck et al. 1967:72.

Records: **KANE**: Kanab (G58). **SUMMIT**: Echo (BAD).

Smith (1979:1368) lists this species as southwestern United States, including Colorado and Arizona, nesting under stones in dry, sunny localities between 5000 and 9000 ft. Gregg (1963:413) lists it from Colorado between 5947 and 8500 ft under rocks in a variety of habitats, predominantly pinyon-juniper. In Utah it prefers plateaus between 5000 and 8000 ft and nests under stones in desert conditions (Grundmann 1958:163). Two recorded collections in Utah were at

4973 and 5467 ft. Beck et al. (1967:72) found it feeding on dead rodents in one instance in Utah.

Pheidole dentata Mayr

P. morrisi var. *dentata* Mayr, 1886, Verh. Zool.-Bot. Ges. Wien 36:457.

P. dentata: Beck et al. 1967:72.

Records: **GRAND**: Dewey (U). **WASHINGTON**: Toquerville (BAD).

Smith (1979:1369) lists this species from eastern to midwestern United States (no intermountain state is listed), where it nests in soil mounds or under various objects. Beck et al. (1967:72) found it feeding on dead rodents in one instance in Utah.

Pheidole desertorum Wheeler

P. desertorum Wheeler, 1906, Bull. Amer. Mus. Nat. Hist. 22:337; Cole 1942:362; Grundmann 1958:163; Ingham 1959:52; Smith 1979:1369.

Records (Map 22): **GRAND**: Moab (U). **UINTAH**: Red Cloud Loop rd 9.2 mi W U44 (A). **WASATCH**: Hanna 4.4 mi W (A). **WASHINGTON**: Castle Cliff (C42), Virgin City (I59).

Smith (1979:1369) lists this as a western species, including Utah, Arizona, and Nevada, nesting under stones and in small crater mounds. Cole (1966:15) found it in southern Nevada under large stones in various habitats of desert shrubs. Grundmann (1958:163) indicates that in Utah it lives under stones in desert habitats under 4500 ft. Ingham (1959, 1963) found it under rocks in blackbrush, yucca, mesquite, and four-wing saltbush in southern Utah.

Seventy-three ants in two collections were found under rocks, once under the same rock with *Formica argentea* and *F. pallidefulva*. One collection was taken in a grassy meadow. In five recorded Utah localities two were in canyon-montane forest. Recorded elevations range between 2500 and 4000 ft.

Pheidole grundmanni M.R. Smith

P. grundmanni Smith, 1953, J. New York Ent. Soc. 61:144; Smith 1979:1370.

Record: **UINTAH**: Merkeley Park on Ashlet Crk (Sm53) (? = Ashley Crk).

Smith (1979:1370) lists this species only from Utah. It was taken from under a stone in cottonwoods at 6000 ft (Smith 1953:144).

Pheidole hyatti Emery

P. hyatti Emery, 1895, Zool. Jahrb. Syst. 8:289; Ingham 1959:53; Beck et al. 1967:72.

Records: **IRON**: New Harmony (I59). **KANE**: Adairville (BAD). **WASHINGTON**: Grafton, Rockville (BAD).

Creighton (1950) and Smith (1979:1370) list two forms of this species from midwest to western United States, including Colorado and Nevada. The Utah form is likely *hyatti*. Hunt and Snelling (1975:21) list it from Arizona. Gregg (1963:419) lists it between 5500 and 5900 ft under rocks in grassy habitats in Colorado. Ingham (1959) found it under rocks in oak, pinyon-juniper, rabbitbrush, and sagebrush in southern Utah.

None of four recorded Utah habitats were in montane areas. Four recorded elevations were between 3660 and 6000 ft. Beck et al. (1967:72) found it feeding on dead rodents in three instances in Utah.

Pheidole pilifera Cole

P. pilifera artemisia Cole, 1933, Ann. Ent. Soc. Amer. 26:616; Rees and Grundmann 1940:4; Cole 1942:362; Creighton 1950:187; Ingham 1959:53; Smith 1979:1372.

Records (Map 22): **EMERY**: Hideout Cyn nr Green River (U). **GARFIELD**: Boulder (U). **SALT LAKE**: Big Cottonwood Cyn (U). **SEVIER**: Salina Cyn nr Fremont Jct (U). **UINTAH**: Gusher (C42). **UTAH**: Payson (C42), Provo (RG), Provo Cyn (U), Wanrhodes Cyn (KU). **WASHINGTON**: Springdale (C42).

Creighton (1950) and Smith (1979:1372) list four races of this species from eastern to western United States, including Utah, Colorado, Arizona, and Nevada, nesting under stones or in craterlike excavations in open areas where they are associated with *P. inquilina*. The two subspecies that likely occur in Utah may be separated by the surface of the occiput of the major, which has prominent rugae on *artemisia*, whereas on *coloradensis* the surface is finely and contiguously punctate. Gregg (1963:422) lists this species from Colorado between 5100 and 8500 ft under rocks in a variety of habitats, predominantly in pinyon-juniper. Cole (1966:15) found it in southern Nevada under large stones in pinyon-juniper. He indicates its habitat in Utah as sagebrush (1942:362). Wheeler and Wheeler (1963) found it frequently under rocks in North Dakota. Ingham (1959) found it under rocks in sagebrush in southern Utah. In 10 recorded Utah habitats it was taken 3 times in montane forest. In 11 recorded elevations it was about equally distributed between 3900 and 7000 ft, twice over 7000.

Pheidole sitarches Wheeler

P. soritis Wheeler, 1908, Bull. Amer. Mus. Nat. Hist. 24:439.

P. sitarches soritis: Creighton 1950:190; Cole 1956:116; Ingham 1959:53; Allred and Cole 1979:99; Smith 1979:1373.

Records (Map 23): **KANE**: Glen Cyn City (AC). **UINTAH**: Dry Fk rd 13.4 mi N U121 (A). **UTAH**: Provo (C56). **WASATCH**: Hanna 9.2 mi W (A). **WASHINGTON**: nr Short Crk (Arizona) (I59). **COUNTY UNKNOWN**: Skull Valley (? probably Tooele Co) (C56).

Creighton (1950) lists three and Smith (1979:1373) four races of this species from eastern to western United States, including Utah, Colorado, and Arizona. The Utah subspecies is likely *soritis*, which may be separated from the close Colorado form by the head of the minor, which is striate posteriorly on *soritis* but punctate on *campestris*. Gregg (1963:424) lists this species between 3500 and 4400 ft under rocks in cottonwood-willow and grassy habitats in Colorado. Ingham (1959, 1963) found it in low mounds in bur sage, little rabbitbrush, junipers, and sagebrush in southern Utah. Allred and Cole (1979:99) found it in southern Utah in a variety of desert shrub types, most frequently in ephedra-grass.

Sixty ants in two collections were found under rocks. One was in sagebrush and one was in sagebrush in association with snowberry. In six recorded Utah habitats it was taken twice from montane forest. Three recorded elevations were between 3250 and 5000 ft.

Pheidole virago Wheeler

P. virago Wheeler, 1915, Amer. Mus. Nat. Hist., Bull. 34:401; Ingham 1959:54.

Record: **WASHINGTON**: between Hurricane and Harrisburg Jct (I59).

Smith (1979:1374) lists this species from Texas and Arizona. Ingham (1959, 1963) found it in southern Utah in small crater mounds in creosote bush, bur sage, little rabbitbrush, cholla, marigold, and Russian thistle. In two recorded Utah collections it was taken at 2900 and 3000 ft.

Pogonomyrmex barbatus (M.R. Smith)

Myrmica barbata Smith, 1858, Cat. Hym. Brit. Mus. 6:130.

P. barbatus molefaciens: Olsen 1934:501; Rees and Grundmann 1940:4; Cole 1942:367.

P. barbatus marfensis: Rees and Grundmann 1940:4; Cole 1942:367.

P. barbatus fuscatus: Rees and Grundmann 1940:4; Cole 1942:367.

Records: **EMERY**: Goblin Valley 10 mi E (KU). **WASHINGTON**: St George (O). **WAYNE**: Fruita 5 mi SE (U).

Smith (1979:1353) lists the distribution of this species as eastern United States westward to include Colorado, Arizona, and Nevada, nesting in low to high craterlike mounds. Grundmann (1958:162) designated it as a southern Utah and northern Arizona desert form, nesting in low craterlike mounds in sandy soil. Cole (1968:56) believes that the St. George (Washington County) record for Utah listed by Olsen (1934) may represent a sparse population of short duration. Cole's distribution map (p. 57) shows it considerably east and south of Utah.

Pogonomyrmex brevispinosus Cole

P. brevispinosus Cole, 1968, Univ. Tenn. Press, p. 89.

Record: **KANE**: Wahweap (KU).

Smith (1979:1354) lists this species from western United States, including Nevada, nesting in low crater mounds. Its occurrence in Utah is questionable.

Pogonomyrmex californicus (Buckley)

Myrmica californica Buckley, 1867, Proc. Ent. Soc. Phila. 6:336.

P. californicus: Olsen 1934:502; Rees and Grundmann 1940:5; Cole 1942:367, 1968:120; Creighton 1950:123; Grundmann 1958:162; Ingham 1959:41; Smith 1979:1356.

Records (Map 23): **KANE**: Glen Cyn Res, Kanab (G58). **SAN JUAN**: Hole-in-the-Rock Cyn (U). **WASHINGTON**: Beaver Dam Wash (I59), Hurricane (RG), between Hurricane and Harrisburg Jct (I59), Leeds, Leeds Cyn (KU), Santa Clara (US), Santa Clara Crk (KU), Shivwits Indian Res (I59), Snow Cyn (KU), St George (O), Veyo (I59), Virgin, Washington (KU).

Smith (1979:1356) indicates the range of this species as primarily southwestern United States, including Arizona and Nevada, in circular or semicircular craters of loose sand. Cole (1966:4) states that in southern Nevada its nests are craterlike, occurring principally in hopsage-matrimony vine and Russian thistle habitats. He (1968:121) shows it in extreme southern parts of Utah essentially west of the Colorado River and in much of Arizona and Nevada. Grundmann (1958:162) designates its distribution in Utah as below 4000 ft, basically a Lower Sonoran form. Ingham (1959) indicates its habitat in southern Utah as conical mounds in creosote bush, sagebrush, and juniper. None of its Utah collections were in canyon-montane areas. In 16 recorded elevations it was between 2500 and 4973 ft, 9 under 3000.

Pogonomyrmex imberbiculus Wheeler

P. imberbiculus Wheeler, 1902, Amer. Nat. 36:87; Ingham 1959:46; Allred and Cole 1979:99.

Records: **KANE**: Glen Cyn City (AC). **WASHINGTON**: Hurricane (I59).

Smith (1979:1357) lists this species from midwest to western United States, including Colorado, Arizona, and Nevada, nesting under stones or in small craters in open areas. Gregg (1963:336) lists it at 4800 ft in saltbush habitats in Colorado. Cole (1968:168) shows it in isolated collections in southeastern Nevada and Arizona only in the extreme southeastern corner. He states that in southern Nevada it nests under stones in hopsage and matrimony vine (1966:6). Ingham (1959, 1963) designates its habitat in southern Utah as soil without mounds in creosote bush, blackbrush, yucca, cholla cactus, and bur sage. Allred and Cole (1979:99) found it in a saltbush-sagebrush association in southern Utah. Three Utah collections were between 3250 and 3500 ft.

Pogonomyrmex maricopa Wheeler

P. californicus maricopa Wheeler, 1914, Psyche 21:155.

P. maricopa: Ingham 1963:47; Cole 1968:138; Smith 1979:1356.

Records (Map 23): **JUAB**: Chicken Crk Res (KU). **MILLARD**: Sutherland (US). **WASHINGTON**: Hurricane (BY), Leeds, Leeds Cyn (US), Santa Clara (KU), St George (BY), Washington (KU).

Smith (1979:1356) lists this species from western United States, including Utah, Colorado, Arizona, and Nevada, nesting in crater-like mounds. Gregg (1963:327) lists it at 4600 ft in weedy areas in Colorado. Cole (1968:139) shows it across extreme southern Utah extending northward along the Colorado River drainage and southward into much of Arizona, as well as southwestern Nevada. Ingham (1959, 1963) found it in sand sagebrush and little rabbitbrush in southern Utah.

Eight recorded Utah habitats were in desert areas between 2500 and 5000 ft, mostly at lower elevations. Its occurrence in Juab and Millard counties is questionable; such records likely are *occidentalis*.

Pogonomyrmex occidentalis (Cresson)

Myrmica occidentalis Cresson, 1865, Proc. Ent. Soc. Phila. 4:426.

P. occidentalis: Olsen 1934:507, 509; Rees and Grundmann 1940:5; Cole 1942:365; 1968:94; Beck et al. 1967:72; Knowlton 1970:211, 1975:7; Allred and Cole 1979:99; Smith 1979:1355.

P. occidentalis utahensis: Olsen 1934:509; Cole 1942:365.

P. occidentalis comanche: Creighton 1950:128; Grundmann 1958:162; Ingham 1959:44.

P. occidentalis occidentalis: Grundmann 1958:162.

Records (Map 24): **BEAVER**: Beaver (RG), Lund 35 and 49 mi N, Milford 1.3 mi N, and 11.5 and 26.7 mi W (A), Wildcat Cyn (C42). **BOX ELDER**: Blue Crk (City), Bovine (C42), Brigham (O) and 0.9 mi E (A), Collinston (C42), Corinne (US) and 6.1 and 16.1 mi W, Deweyville 0.3 mi N (A), Garland, Hansel (US), Hansel Mts (K70), Hardup, Howell (C42), Kelton 17.2 and 28.5 mi SW (A), Lampo (US), Locomotive Spngs, Lucin (C42), Promontory 1.3 and 10.3 mi W (A), Promontory Pt (C42), Snowville (O) and 7.7, 19.1 and 30.7 mi S (A), Thicket (KU), Wendover 28 mi N (A), Willard (C42) and 1.5 mi S (A). **CACHE**: Blacksmith Fk Cyn (KU), Cache Jct (C42), Cornish (KU), Cove (C42), Leeds Cyn (KU), Logan (C42), Logan Cyn (KU), Mendon, Providence (C42), Smithfield 0.5 mi N (A), Mt Sterling (C42). **CARBON**: Argyle Cyn, Kenilworth (U), Myton rd 5 and 22.7 mi E US6, Price 2.2 mi S (A) and 20 mi S (WU), Wellington 5 mi S, and 5 and 10 mi NE (A). **DAGGETT**: Radosovich Ranch (BAD). **DAVIS**: Farmington (C42), Kaysville (O), Layton 1.5 mi S (A). **DUCHESNE**: Blue Bench, Currant Crk (C42), Duchesne 5.3 mi E, 2 mi N (A) and 11 mi W (WU), Hanna 1.5 mi W, Myton rd 33.5 mi E US6, Neola 6.2 mi S, Tabiona 11.6 mi E, Wellington rd 7.2, 17.3 and 27.4 mi S US40 (A). **EMERY**: Buckhorn Res (BY), Emery 4.5 mi N and 4.9 mi S, Ferron 1.4 mi N (A), Goblin Valley and 10 mi E (KU), Green River (C42), Hanksville 16 mi N (KU), Hideout Cyn nr Green River (U), Huntington (US) and 1.7 mi S, Orangeville 3 mi W, Wellington 15, 26, 36 and 46 mi S (A). **GARFIELD**: Antimony 5.8 and 27.6 mi S (A), Boulder Mts, Carcass Crk (on Boulder Mt) (U), Bryce Cyn Nat Park (US), Escalante 20 mi S and 20 mi E (U), Henry Mts (G58), Hanksville 26.6 mi S (A), Osiris (U), Rubys Inn (US), Tropic 3.3 mi E, Jct U12 and U63 0.5 mi E (A). **GRAND**: Arches Nat Park, Cisco (BY) and 1.5 mi E, Crescent Jct 5 and 18.8 mi S, and 6, 37 and 47 mi E (A), Dewey (U), Green River 5 and 16 mi E (A), Moab (G58) and 1.5 mi S (A), Thompson (C42). **IRON**: Beryl 1 mi NE (A), Cedar City (RAU), 3.7 mi E, and 6.3, 16.8 and 27 mi W (A), Columbia Iron Mine 7 mi W (159), Enoch (RAU), Iron Mt (US), Little Pinto

(KU) and 3 mi NE (US), Lund 8.6 and 19 mi N, Modena 5.3 and 8.7 mi W, and 10.4 and 25 mi NE, Newcastle 7.2 and 17.2 mi W (A). **JUAB**: Callao 7.8 mi E, Eureka 0.5 mi E and 3.7 mi S (A), Fish Spngs (BY), 0.8 mi N, and 1, 10.6, 20.8 and 30.8 mi E, Gandy 10.1 mi N (A), Indian Farm Cyn (in Deep Crk Mts) (U), Jericho (BY), Levan 6.9 mi N and 10 mi S, Lynndyl 11.5 and 21.5 mi N, Nephi 3 mi N, and 5.5, 12.1 and 23 mi W (A), Pony Express Sta (US), Tintic (C42), Topaz Mt and 5 mi NW (US), Trout Crk (City) 2.8 mi N (A). **KANE**: Adairville (BAD), Cannonville 8.7, 31.3 and 41 mi S (A), Escalante River (BY), Glen Cyn City (AC), Johnson Cyn (BY), Kanab (O), 4–7 mi N (I59), 4 mi E (KU), and 5, 20.4, 31 and 41 mi E (A), Long Valley Jct 2 mi W (I59) and 0.5 mi S, Mt Carmel Jct, Orderville 2 mi N (A), Paria (BY), Wahweep Cmpgnd (US). **MILLARD**: Black Rock (KU), Delta (BY) and 0.5 mi W (A), Deseret (US), 3 mi S (KU) and 30 mi S (US), Fillmore (C42), Hinckley 4.8, 14.7, 24.9, 35, 45, 58.1 and 69.6 mi W (A), Holden, Kanosh (US), Lynndyl 2 mi S (A), Meadow (C42), Milford 16.3, 31.5, 46.3 and 61.3 mi N (A). **PIUTE**: Antimony 4.8 mi N (A), Grass Valley (KU), Kingston (A), Marysvale (BY) and 4.1 mi S (A). **RICH**: Garden City 1.6 mi N, Randolph 2.3 and 5.3 mi N, Woodruff and 4 mi W (A). **SALT LAKE**: Big Cottonwood Cyn, Ft Douglas, Granite, Point-of-Mt (C42), Riverton 2.6 mi S (A), Salt Lake City (C42), Sandy (O). **SAN JUAN**: Abajo Mts (G58), Blanding 6.7 mi N (A) and 8 mi N (U), Blue Crk, Bluff (C42) and 0.6 and 11.6 mi S (A), Jct Colorado and San Juan rivers (U), La Sal, La Sal Jct (RG) and 1.6, 11.7 and 23.1 mi S, Mexican Hat 8.2 mi S, Moab 12 mi S, Monticello 0.5 mi N, Jct U95 and U261 7.7 mi W, Jct U261 and US163 9.4, 19.6 and 29.9 mi N (A), Squaw Flat Cmpgnd (in Canyonlands Nat Park) (WU). **SANPETE**: Ephraim and 3 mi N (A), Ephraim Cyn (U), Fairview (BY) and 16.5 mi N, Freedom 0.5 mi N, Gunnison (A), Indianola (BY), Levan 20 mi S (A), Majors Flats (KU), Mt Pleasant (C42) and 0.5 mi N, Nebo Loop rd 6.3 mi E Jct U11 (A), Wales (RG). **SEVIER**: Axtel 4 mi S, Big Rock Candy Mt (A), Elsinore (C42), Fremont 18.9 and 28.6 mi N, Richfield 2.3 and 7.5 mi S (A). **SUMMIT**: Coalville (U), Francis 1 mi E, Wyoming brdr 1.5 and 10.4 mi W on I80 (A). **TOOELE**: Clover 1 mi W (A), Delle (O) and 2, 12 and 22 mi W (A), Dugway (BY) and 5 and 10 mi E, Faust 1.5 mi W and 3.6 mi E (A), Grantsville (O) and 2 and 12.1 mi W (A), Iosepa (C42), Johnson Pass (US), Little Valley (C42), Lookout Pass (BY), Low, Orrs Ranch (C42), Rowley Jct 0.5, 10.8, 21 and 31 mi S, Simpson Spngs 4 and 14 mi E (A), Stansbury Island (C42), Tooele (O), 1 mi S and 3.3 mi W, Jct U36 and U73, Vernon, Wendover 10.3, 13.3, 14.5 and 23.1 mi N (A), S Willow Cyn (U). **UINTAH**: Bonanza 3 mi S (KU), 8 and 21 mi S, and 5 and 15 mi N, Dry Fk rd 9.4 mi N U121 (A), Ft Duchesne (C42), Gusher 4 mi E (KU), Jensen 5.5 mi W and 7.5 mi E, Lapoint 1 and 10.7 mi E (A), Ouray (C42), Split Mt, Vernal (BY), 6 mi E (KU) and 5 and 10 mi N (A). **UTAH**: Cedar Fort (U) and 1.9 mi N (A), Elberta (C42) and 1 mi W, Fairfield 3.3 mi W (A), Lehi (O) and 4.4 mi W (A), Orem, Provo, Provo Cyn (BY), Santaquin (C42), 1.5 mi N, 1.5 mi W and 0.5 mi S, Springville 2 mi S, Thistle 2.7, 3.6, 7.7, 9 and 14.6 mi E (A), W Utah Lake (BY). **WASATCH**: Francis 5.4 mi W, Hanna 4.4 mi W (A), Heber (U) and 2.3 mi W (A), Soapstone Cyn (U). **WASHINGTON**: Grafton (I59), Hurricane (RAU), Leeds (RG), Mt Meadow, New Harmony (BY), Pine Valley (City) (I59), Pinto, 3 mi S (US) and 5 mi S (KU), Rockville, Santa Clara (I59), Springdale (C42), St George (RG), Virgin, Zion Nat Park (O). **WAYNE**: Capitol Reef Nat Park, Fruita 5 mi SE (U), Hanksville 3, 17.4 and 27.2 mi W, and 7 and 16.7 mi S, Torrey 3.7 mi E and 5.3 mi W (A). **WEBER**: Little Mt (C42), Ogden (O), Ogden Cyn (BY), Riverdale (C42), Jct U39 and U166 3.3 mi E, Woodruff 34.8 mi W (A). **COUNTY UNKNOWN**: Brush Crk (RG) (prob Uintah Co), Westville (C42) (prob Wellsville in Cache Co).

Smith (1979:1355) indicates this species as a western one, including Utah, Colorado, Arizona, Nevada, Idaho, and Wyoming. Gregg (1963:331) lists it from Colorado between 3500 and 9000 ft in a variety of habitats, predominantly in pinyon-juniper, sagebrush, and grass. Ingham (1959, 1963) indicates its habitat in southern Utah as a variety of shrub types. Allred and Cole (1979:99) found it in southern Utah in a wide variety of desert shrub types, most frequently in grass-hopsage and ephedra-grass-blackbrush-hopsage associations. Rees and Grundmann (1940:5), Cole (1942:365), and Grundmann (1958:162) list it from a variety of situations in Utah.

Thirty-two hundred ants in 211 collections were taken from 87 different plant types or associations. Eighty-one collections were taken in sagebrush or sage associations. Fifty-two collections were in grass or grass associations other than with sagebrush. Twelve collections were from pure stands of greasewood, and 10 collections from greasewood with other plants except sagebrush or grass. Seventeen collections were from halogeton associated with other plants except sagebrush or grass. Thirteen collections were from shadscale in association with other plants except sagebrush or grass. Only 8 collections were taken from rabbitbrush associations other than with sagebrush or grass, and only 5 collections from blackbrush. Only 2 collections were taken in juniper and/or pinyon where other plants were not present, but 19 collections where sagebrush was associated.

This species commonly inhabits the shoulders and barrow pits along roads. Whenever sedges, meadow grass, or salt grass were present alongside the roads, I never found colonies of this species. Apparently it does not like the saline environment in this type of situation. Colonies were seldom found in heavy clay soils, but occasionally in lighter clays.

Unstable sandy soil does not support this species, apparently because of the shifting potential of the sand from frequent winds. From just west of Hinckley in Millard County for a distance of about 14 miles westward, the soil is alkaline clay with greasewood, saltbush, and shadscale. In this area harvester mounds were found only along the shoulder of the highway where a gravel substrate was present. None were found on the alkaline flats until the greasewood and saltbush were replaced by shadscale and desert pavement. Between Sagecreek Junction and Laketown in Rich County, a distance of 10 miles where the soil is a reddish clay loam, not a single harvester mound was seen. Typical mounds were not seen between Blanding and Bluff in San Juan County, where the elevation dropped from 6100 to 4300 ft in 70 miles, and only those of *P. rugosus* were present. South of Bluff past Mexican Hat both mound forms and species were present, but *occidentalis* was not as common as in other areas. About 11 miles north of Mexican Hat following highway U261, Cedar Mesa lies at 6500 ft. Mounds of *rugosus* were found up to its base but were replaced on top by *occidentalis*. Ants of *rugosus* occur infrequently further westward along U95, where the elevation drops back to under 4600 ft.

In the 375 localities listed, only 31 were in montane forest. The 119 recorded elevations varied from 2750 to 9000 ft, 86 of them between 4000 and 6000. Only 21 were over 6000 ft, 2 over 8000.

There were 213 typical mounds observed. In 5 cases two main mounds were joined and apparently inhabited by the same colony. In only one instance did I find a colony occupying three joined mounds. In a greasewood habitat 17.2 mi southwest of Kelton in Box Elder County a colony was found with three joined, small linear mounds that had a total of nine entrances. A typical mound in an alkali-greasewood flat 7.8 mi east of Callao in Juab County was covered with black chips of desert pavement. In an area 4.9 mi south of Emery along U10 at 6000 ft in Emery County in greasewood, grass, and Russian thistle several mounds were completely covered with a layer of black gravel, which undoubtedly was carried from the shoulder of the road where it had been used for surfacing. Some such mounds were as far as 60 ft from the road. Four mounds on an east-facing slope at the north edge of Woodruff at 6400 ft in Rich County in sagebrush were covered with large gravel, the particles much larger than seen on other harvester mounds elsewhere in the state. These also were elongate and ridged, not the symmetrical cones like the typical harvester mounds. A low mound was found two feet from the asphalt 14.7 miles west of Hinckley in Millard County, with the opening at the base on the northeast side. The area around the entrance was coated with a hardened amber material resembling baltic amber or shellac. Apparently this was deposited from the feet of the workers over a long period of time, perhaps picked up as a distillate from the hot surface of the adjacent asphalt. No other situation of this type was observed with any other mound over the state. A mound in another area had two rodent burrows in it, with a gopher snake curled in one of them.

Food storage of seeds was frequently found in the upper part of the mounds, usually within a few inches of the top.

In northwestern Utah around Kelton in Box Elder County, where the range of three species of harvesters overlaps, *occidentalis* are much larger than most *salinus*, but about the same size as *owyheei*.

To see the angled basal tooth on the mandible, one sometimes must study a series for best observation of open mandibles. On some specimens all teeth of both mandibles are well developed and the basal tooth on both sides is well developed and distinctly angled. On other specimens the basal tooth on one side may be vestigial, in which case the other teeth on the same mandible may be much reduced, almost lacking in some cases, or moderately well developed in others. The basal tooth on the other mandible, however, is well developed and distinctly angled. Frequently the angle is not distinct as such, but the basal tooth forms a gentle curve instead. In series 388, taken 3.3 miles west of Tooele alongside highway U112 in Tooele County, one ant has eight teeth on the right mandible and seven on the left. The basal tooth is offset on both mandibles. In series 122, taken 37 miles east of Crescent Junction alongside highway 170 in Grand County, most specimens have a basal tooth that is only slightly angled with the posterior border of the mandible, forming almost an equal curvature. In series 305, taken five miles south of Crescent Junction alongside highway US163 in Grand County, most specimens have a basal tooth that is not as offset as most other typical *occidentalis* scattered throughout Utah. On some of these specimens one side of the mandible is almost straight, whereas on the other, or on both sides on some specimens, the basal tooth forms a slight gentle curve. Other characters, such as the rugae and puncta on the head and the shape of the base of the antenna, are typical characters. In series 113, taken 26 miles south of Wellington alongside highway US6 in Emery County, the basal tooth on both mandibles is well developed but the posterior margin of the mandible is almost straight without an angle. A colony (series 115), taken 46 miles south of Wellington in Emery County in halogeton in mid-July, consisted of many workers with a few immatures but no winged forms. In a series of 30 workers examined, the basal tooth on many is almost in a straight line with the basal margin of the mandible, and on a few it is in straight alignment. Other characteristics are typical of *occidentalis*. In series 199, taken one mile east of Francis in Summit County the basal tooth is often reduced on one mandible. On some specimens where it is reduced, the border of the reduced tooth is not at a distinct angle, but almost straight. In series 354, taken 17.4 miles west of Hanksville on highway U24 in Wayne County, many workers have essentially a straight mandibular border; others have an angled basal tooth at least on one side, but not as drastically as typical *occidentalis* of other areas of Utah.

On some workers all of the teeth on both mandibles except the two basal ones are worn off so that the inside edge of the mandible is essentially straight except for the two basal teeth, which are typically offset. In series 356, taken 3.7 miles east of Torrey in Wayne County, one worker has both mandibles with no evidence of any teeth. The edge is heavily chitinized, but it appears that all the teeth have been worn off smooth so that the normal toothed edge is perfectly straight, with no indentation showing where teeth should be, even to the offset basal tooth, which is also missing on both sides.

Some intergradation of mandibles occurs in northwestern Utah, mainly between *salinus* and *owyheei*. Most *occidentalis* in that area are typical, but some have atypical mandibles close to *salinus* and *owyheei*. In series 549, taken 17.2 miles southwest of Kelton in Box Elder County, some ants have typical *occidentalis* mandibles, antennae, and petiole pattern; some have mandibles and antennae of *occidentalis*, with a petiole pattern of *salinus*; some have mandibles of *salinus* or *owyheei* and antennae of *occidentalis*, but with a petiole typical of *salinus*.

In 111 mounds where other than workers were found, immatures but no winged forms were found in 20 (18 percent), winged forms only in 47 (42 percent), and both immatures and winged in 44 (40 percent). Immatures and winged forms were found in mounds above normal ground level only between 28 June and 3 August. When immatures were found in the summer they were between two to four inches below the outer surface of the mound in different parts of the mound as oriented to the direction of the sun. This may be optimum for brooding temperatures of the immatures, and they likely are moved periodically by workers as the outside temperature and rays of the sun change.

On 31 July in sagebrush one mile east of Brigham in Box Elder County at 0650, a mound was observed that was still in shade. No ants were outside the mound, but many winged forms were congregated just inside the entrance, probably preparatory for the nuptial flight. Almost as many winged ants as workers were found inside the mound. On the same day in a grass and sunflower habitat 6.1 miles west of Corinne in Box Elder County at 0740, a small mound was observed that was still in shadow. Many winged forms were assembled just inside the entrance, but no ants were outside. The same situation was seen in two other adjacent mounds. In a mound located three miles west of Orangeville at 6000 ft in Emery County in rabbitbrush, greasewood, and herbs near an irrigated farm, winged forms were much more numerous than workers on 31 July and were found near the opening to the nest, whereas the fewer workers were deeper in the mound.

Apparently the winged forms were nearing their swarming time.

Winged forms vary in depth in the mound, but frequently can be seen "peeking" from the openings. Callow (newly emerged) workers frequently were found mixed with the winged forms and were the principal workers to rescue immature stages when the nest was disturbed. Winged females are much more active in trying to hide or escape when disturbed than are winged males. The winged females frequently aid the callow workers in rescuing the immature forms, but I never once saw a winged male performing that task.

One colony taken 41 miles east of Kanab in Kane County was in a low mound in rabbitbrush, matchbrush, and saltbush. Moderate numbers of workers were present, but no immature or winged forms. These ants behaved differently than typical *occidentalis*—they were not aggressive and did not swarm toward the intruder when disturbed, but simply scurried around almost at random. Their abdomens were darker (almost blackish) than the amber unicolor of typical *occidentalis*. Forty-five miles west of Hinckley, alongside highway US6-50 in Millard County, a colony was found in a typical *occidentalis* mound with the opening at the base on the southeast side. These ants behaved similarly to *salinus*. They were not aggressive but tried to hide when disturbed. A mound covered with thick detritus and occupied by *occidentalis* was found 7.7 miles west of junction U261 on U95 in San Juan County in sagebrush, pinyon, and juniper. Ants of *Conomyrma insana* were abundant on the mound, crawling on and between the sticks. No nest openings of these small ants could be seen, nor were any of their nests found in the vicinity. No interaction between the two species was observed as they intermingled on the mound. A large, flattened mound was found in rabbitbrush, sagebrush, and juniper 19 miles north of Lund on the road to Pine Valley in Iron County in late July at 6700 ft. Workers were transporting sand particles from its opening. Many workers, immature, and winged forms were found in the mound. Nine small mounds occupied by *Conomyrma insana* were on the harvester mound. No apparent competition or interaction was seen between the two species as they intermingled in their scurryings.

Beck et al. (1967:72) found *occidentalis* feeding on dead rodents in only two instances in Utah.

Pogonomyrmex owyheei Cole

P. occidentalis owyheei Cole, 1938, Amer. Midl. Nat. 19:240.

P. owyheei: Cole 1968:102; Knowlton 1970:211, 1975:7; Smith 1979:1355.

Records (Map 24): **BOX ELDER**: Cedar Crk (City) (K75), Cedar Hill (US), Curlew Valley (K70), Hansel Mts, Hardup, Kelton (K75), 6 mi N (US), 8.3 mi E, 70.4 mi SW (A), and 12 mi NW (KU), Kelton Pass (K75), Kelton rd 5 mi E U30 (A), Locomotive Spngs (K75), Park Valley (City) 10 mi E (KU), Snowville (K75) and 1 mi W, Jct U30 and U42 and 3.8, 5.8, 6.1 and 6.7 mi N (A), Wildcat Hills (K75). **EMERY**: Goblin Valley, Hanksville 16 mi N (KU). **GRAND**: Moab, Thompson (KU). **JUAB**: Fish Spngs (KU). **MILLARD**: Black Rock (KU). **WASHINGTON**: Rockville, Santa Clara Crk, St George, Virgin, Zion Nat Park (KU).

Smith (1979:1355) lists this species as western United States, including Utah, Nevada, Idaho, and Wyoming, nesting in earthen mounds. Allred and Cole (1971:239) found it in Idaho abundantly in associations of rabbitbrush-sagebrush-grass, less commonly in other shrub associations. Knowlton (1975:7) found it associated with sagebrush and rabbitbrush in northern Utah.

There were 260 ants taken from typical conical mounds in nine collections. Immatures and winged forms were found in four mounds in late July. In two of the mounds only female alates were found. Seven collections were taken in sagebrush: two in association with grass and one with grass and rabbitbrush. Two collections were taken in greasewood. In a greasewood area alongside an old railroad bed 8.3 miles east of Kelton in Box Elder County, a colony was adjacent to several colonies of *salinus*. Elevations of *owyheei* in Utah are between 4310 and 5600 feet in desert habitats.

On 31 July in Box Elder County two mounds were seen wherein many winged forms were concentrated just inside the entrance. At one mound several winged females came out of the entrance but quickly reentered when I approached. In series 558, taken 5.8 miles north of highway U30 along U42 in Box Elder County, the ants were not as aggressive as *occidentalis* nor as prone to hide as *salinus*, but their behavior was closer to that of *salinus*. Fewer could be enticed to come out of the entrance than is the case with *occidentalis* when air is blown into the entrance. Workers of *occidentalis* literally swarm out in such a reaction.

In series 560, taken 6.7 miles north of the junction of highways U30 and U42 alongside U42 in Box Elder County, many specimens have a broadly rounded thorax, not flattened. The superior lobe of the scape base is somewhat variable. On several specimens on one side the lobe has a collar that is extended superiorly, but with no up-curvature as on typical *occidentalis*. On the other side of the same specimens the lobe is similar to *salinus*, angular and rounded, without the collar extension. Both segments of the petiole lack the typical *salinus* transverse striae, although faint subparallel striae are on the posterior half of the petiole, whereas the postpetiole lacks such striae on a few specimens. Most specimens in other series have the superior lobe of both antennae with an extension of the collar. In series 559, taken 0.6 mile southeast of series 560 above, at least one specimen has a superior lobe of the scape base that is almost typically *salinus*—rounded without the collar extension. On the other antenna the superior lobe is angled and rounded without the collar extension. In series 557, which was taken six miles southeast of the above collections, one specimen has typical *owyheei* antennae and mandibles with an atypical salinus *petiole*.

The records of this species from Juab, Millard, Emery, Grand, and Washington counties most likely are errors of identification of aberrant specimens of *occidentalis*, wherein the offset basal tooth of the mandible is not typical. Such variations were discussed under *occidentalis* previously.

Pogonomyrmex rugosus Emery

P. barbatus rugosus Emery, 1895, Zool. Jahrb. Syst. 8:309; Rees and Grundmann 1940:5; Cole 1942:366; Creighton 1950:120; Grundmann 1958:162; Ingham 1959:39.

P. rugosus: Cole 1968:70; Allred and Cole 1979:99; Smith 1979:1354.

Records (Map 23): **EMERY**: Green River (RG). **GRAND**: Arches Nat Park (BY), Dewey (U), Green River S of (KU), Moab (U), Thompson (C42). **KANE**: Glen Cyn City (AC), Kanab (G58) and 4 and 40 mi E, Wahweap (KU). **SAN JUAN**: Abajo Mts (U), Blanding 6.4 and 12.2 mi S (A), Bluff (KU) and 0.6 and 11.6 mi S (A), Four Corners (US), Goulding Mt (RG), Mexican Hat (U), Monument Valley (KU), Navajo Bridge (on Highway 89) (G58), Jct U95 and U261 35 and 40.4 mi W, Jct U261 and US163 3.7 mi N (A). **UTAH**: Silver Lake Flat (A). **WASHINGTON**: Hurricane (RG), Harrisburg Jct 2 mi W (159), Leeds Cyn, Rockville, Santa Clara, Snow Cyn (KU), Springdale (WU), St George (O), Virgin City, Zion Nat Park (159).

Smith (1979:1354) lists this species from midwest to western United States, including Utah, Colorado, Arizona, and Nevada, nesting in the soil in a flattened gravel disc. Gregg (1963:323, 327) lists it between 3600 and 8500 ft in sagebrush, saltbush, conifers, juniper, oak, manzanita, grass, and greasewood areas in Colorado. Cole (1968:71) shows it across all of extreme southern Utah, arching northward near the borders as it extends into central and southeastern Nevada and central western Colorado. He states that in southern Nevada its nests consist of low gravel mounds or discs, commonly found in hopsage-matrimony vine, shadscale, blackbrush, creosote bush, Russian thistle, and other mixed shrubs (1966:5). Ingham (1959, 1963) indicates its habitat in southern Utah as flattened pebble mounds in creosote bush, sagebrush, pinyon-juniper, blackbrush, joshua trees, bur sage, little rabbitbrush, four-wing saltbush, and shadscale. Allred and Cole (1979:99) found it in southern Utah in several desert shrub types, most commonly in grass communities.

There were 160 ants in seven collections taken from low crater mounds not over four inches high and 18 inches to two feet in diameter. Eleven ants in one collection were taken from under a log. No typical cleared area occurs around these mounds. Two collections were taken in blackbrush, one in association with grass and Russian thistle. Two collections were in greasewood: one in association with Russian thistle and one with grass, herbs, and sagebrush. One collection was taken in herbs, one saltbush, one grass and matchbrush, and one grass near aspen. In 36 recorded Utah habitats two were in montane areas. In 27 recorded elevations between 2500 and 7500 ft, 21 were between 3000 and 5000, two over 7000. These ants are not as aggressive as *occidentalis*, and some attempt to hide when disturbed. Ants of one colony found in a habitat of blackbrush, Russian thistle, and grass 35 miles west of U261 along U95 in San Juan County were harvesting grass seeds on 30 July and carrying them into their nest.

The record in northern Utah County collected by me is valid. I revisited the exact site a year later, but no ants were present. In the initial collection only 11 ants could be found, and they were at 7450 ft under a small aspen limb on an open west-facing, grassy slope below an aspen grove.

Pogonomyrmex salinus Olsen

P. salinus Olsen, 1934, Bull. Mus. Comp. Zool. 77:498; Knowlton 1970:211, 1975:7.

Records (Map 24): **BEAVER**: Desert Range Exp Sta (BY). **BOX ELDER**: Cedar Crk (City) (KU), Cedar Hill (K75), Curlew Jct, Curlew Valley, Hardup (KU), Kelton (K70), 5 mi SE (KU), 8.3 mi E, 3.3 and 12 mi W, and 39.8, 50.9 and 60.1 mi SW (A), Kelton Pass (K70), Kosmo (K75), Locomotive Spngs (K70), Penrose 7 mi NW, Park Valley (City) 10 mi E (KU), Promontory 20.3 mi W (A), Snowville (K75), Wildcat Hills (US). **IRON**: Cedar City (RAU). **JUAB**: Callao 5 and 10 mi E (A), Fish Spngs (KU), Gandy 10.1 mi N (A), Topaz Mt (KU), Trout Crk (City) 12.3 mi N (A). **MILLARD**: Gandy 1.7 mi N, and 3.2, 3.5, 8.5, 13.6, 17.2 and 20.1 mi S, Gandy rd 0.5 mi N US6-50, Hinckley 14.7 mi W (A). **TOOELE**: Knolls 3, 3.5, 13, 16.8 and 22.8 mi W, Wendover 5.5 mi E (A).

Smith (1979:1355) lists this species from western United States, including Nevada, nesting in a low craterlike mound in pinyon-juniper areas. Cole (1968:107) shows it along the eastern border of Nevada in the northern half of that state but not next to Utah in the southern third of Nevada. He indicates that in southern Nevada it is one of the dominant ants of the pinyon-juniper, replacing *occidentalis* at higher elevations, contacting but not overlapping the range of the latter. The nests are saucerlike depressions in cleared areas (1966:6). Knowlton (1975:7) found it associated with sagebrush in northern Utah.

There were 510 ants in 20 collections taken from low crater mounds. Sixty-five ants in 4 collections were taken from low, flat mounds, and 40 ants in 2 collections were taken from ground burrows without mounds. Eighty ants in 3 collections were taken from mounds that were larger than the others and typically shaped like those of *occidentalis*; however, all had openings at the top, only one with a crater. Immatures were found in 5 nests and winged forms in 10. Both immatures and males were found together in 4 nests. Fourteen collections were taken in greasewood: 5 in association with halogeton, 2 shadscale, and one halogeton and shadscale. Five collections were in shadscale, 5 shadscale and halogeton, one halogeton, one halogeton and saltbush, and one pickleweed. Two collections were taken on the shoulder of a road where no vegetation was present. All 44 recorded Utah habitats were in desert areas between elevations of 4222 and 5834 ft.

These ants are not aggressive and attempt to hide when disturbed, exhibiting little attempt to rescue exposed immature forms. In only two colonies was there indication of aggression. In two colonies alongside a paved highway, kernels of wheat were found.

This species apparently extends alongside highway US6-50 70 miles eastward from the Nevada border to within about 14 miles of Hinckley in Millard County. At intervals westward from Hinckley the soil is an alkaline clay with greasewood, shadscale, and saltbush. No harvester mounds, even of *occidentalis*, were seen in these areas except along the shoulder of the road where a gravel substrate was present. When the greasewood, saltbush, and alkaline-clay are replaced by desert pavement and shadscale, harvester mounds are present. For 8 miles north of US6-50 alongside the Nevada border toward Gandy, only two mounds were seen in the alkali-clay greasewood habitat up to the shadscale of the bajada. In the valley east of Kelton in Box Elder County in northwestern Utah, where the soil is not as alkaline or clay, harvester mounds are common in greasewood alongside the highway. However, the mounds there are small and frequently covered with greasewood detritus. For many miles southwest of Kelton in the greasewood-shadscale-halogeton habitat, no mounds of *salinus* were seen except those occasionally in the middle of the hardpacked dirt road.

This species with its typical low crater mounds extends along US80 from about 1.5 miles east of Knolls in Tooele County westward to Wendover. Typical *occidentalis* with its higher pyramid mounds extends eastward along I80 from about 3 miles west of Knolls. In this overlap area of about 4.5 miles are some mounds that are intermediate between the two species types—higher pyramid mounds with top craters. In the area east of the typical crater mounds for a distance of about 1.5 miles, no typical crater mounds were seen but frequent intermediate types were present. The intermediate types were not seen eastward from about 3 miles east of Knolls.

Between 40 and 60 miles southwest of Kelton in Box Elder County the only mounds found were in the middle of the hard-packed dirt road. Between about 25 and 70 miles west of Hinckley in Millard County along US6-50, wherever mounds of *occidentalis* were abundant no colonies of *salinus* were found. In a halogeton-shadscale area 12.3 miles north of Trout Creek City in Juab County, colonies of *occidentalis* were abundant in the same area as *salinus.*

In an alkali-greasewood area five miles east of Callao in Juab County a completely flat mound was covered with a dense concentration of black chips of desert pavement. In the same habitat five miles farther east a typical mound was covered with black chips of desert pavement, including the inside of the crater.

In a shadscale area 14.7 miles west of Hinckley in Millard County a mound was typical *occidentalis* in shape except that the opening was at the top. However, the mound lacked the crater typical of *salinus.* These ants demonstrated typical *salinus* behavior of nonaggressiveness and attempts to hide when disturbed. The mound was conspicuously covered with black chips of gravel that were common in the vicinity as desert pavement. However, the closest source of these to the mound was about 50 ft away. Another mound in the same area was of the same shape but possessed a small crater on the top. This mound was covered by light-colored gravel, probably brought from excavating within the mound. These ants behaved as typical *salinus.* A mound that was an intermediate type—relatively high pyramid with top crater—was found 3.5 miles west of Knolls alongside US80 in Tooele County. The ants behaved as intermediates between *salinus* and *occidentalis*—some tried to escape and hide, whereas others crawled around in a manner typical of *occidentalis.*

In series 395, taken 13 miles west of Knolls along US80 in Tooele County, all of the specimens examined have typical *salinus* straight-margin mandibles, but some have the basal part of the scape more typical of *occidentalis.* Others in the same series have the typical *salinus* scape. In series 397, taken 22.8 miles west of Knolls alongside US80, in Tooele County, two ants have all the teeth rounded and not heavily sclerotized. The distal three teeth are fused together. The basal tooth is not offset and is in straight alignment with the mandibular margin. Two others have the teeth rounded, with the two distal ones fused, but the basal tooth is in straight alignment with the margin of the mandible. In series 405, taken 3.5 miles west of Knolls, the ants have characters typical of both *salinus* and *occidentalis.* The basal tooth is consistently in line with the others, not offset. The superior lobe of the scape in many is more rounded (almost like typical *salinus*) than in *occidentalis,* but many specimens have a superior lobe that is more angled, similar to that of *occidentalis.* In series 510, taken 17.2 miles south of Gandy in Millard County, the ants are typical *salinus* except that, although some have the superior lobe of the scape rounded as is typical of *salinus,* others have a lobe that is more angular like *occidentalis.*

In series 548 there are intergrades between *salinus* and *owyheei.* One specimen has a *salinus* antenna on one side and an *owyheei* antenna on the other, with a typical *salinus* petiole. Another has *salinus* antennae and an *owyheei* petiole; one has *owyheei* antennae and *salinus* petiole. Most others of the series are typical *salinus.* In series 551, taken 39.8 miles southwest of Kelton, two specimens have *owyheei* antennae but *salinus* petioles. In series 546, taken 8.3 miles east of Kelton, some of the ants are typical *salinus* with reference to the superior lobe of the base of the scape, transverse rugae on the petiole, and the postpetiole. A few specimens have the superior lobe of the base of the scape similar to that of *owyheei,* and on these the transverse rugae on the petiole and postpetiole are not as distinct as on typical *salinus,* especially on the anterior half of the postpetiole.

Pogonomyrmex subnitidus Emery

P. occidentalis var. *subnitidus* Emery, 1895, Zool. Jahrb. Syst. 8:310.

P. subnitidus: Allred and Cole 1979:99.

Records: **KANE**: Glen Cyn City (AC). **SAN JUAN**: Mexican Hat 3.2 mi S (A).

Smith (1979:1355) lists this species only from Nevada nesting in craterlike mounds, and Cole (1968:114) lists it from western Nevada. Allred and Cole (1979:99) found it in southern Utah in ephedra-grass associations.

Thirty ants in one collection were taken from a typical *occidentalis*-type mound in an association of matchbrush and Russian thistle. I was stung on the arm by one of the workers, and the reaction was equal to if not more severe than that to *occidentalis*.

Ants of this species are significantly larger than those of *occidentalis*. The head is much darker than *occidentalis*, almost black, and the rugae are much closer together, with a little-beaded appearance. The basal tooth on the mandible is almost curved toward the other teeth, and the inner margin of the mandible is generally straight except that a small hump exists. In series 335, taken 11.6 miles south of Bluff in San Juan County, 24 of the 25 specimens collected have the mandibular teeth worn down, some to the point where no vestiges of teeth are visible. One such specimen has the tips of both mandibles broken off.

Polygerus breviceps Emery

P. rufescens breviceps Emery, 1893, Zool. Jahrb. Syst. 7:666; Rees and Grundmann 1940:10; Cole 1942:385; Creighton 1950:558.

P. rufescens umbratus: Creighton 1950:560; Grundmann 1958:167; Ingham 1959.

Records (Map 25): **CACHE**: Green Cyn, Logan, Logan Cyn (C42), Providence (KU). **GARFIELD**: Boulder Mt nr Boulder (G58). **IRON**: Cedar City (I59). **KANE**: Cedar City 24.3 mi E (A). **SALT LAKE**: Big Cottonwood Cyn (U). **SANPETE**: Chester (RG), Majors Flats (KU). **SEVIER**: Richfield (RG). **UINTAH**: Bonanza (KU).

Smith (1979:1466) lists this species as midwestern to western United States, including Arizona, where it associates with a variety of species of *Formica*. Gregg (1963:638) lists it from Colorado between 5080 and 8900 ft under rocks, logs, and in domes in a variety of habitats. La Rivers (1968:11) lists it from Nevada, where Wheeler and Wheeler (1978:396) found it between 6400 and 10,500 ft. Cole (1942:385) indicates its habitat in Utah as under stones, associated with a variety of species of *Formica*. Grundmann (1958:167) designates it in Utah as typically a mountain form in dry and rocky situations where sagebrush is present. Ingham (1959) found it in southern Utah in pinyon-juniper and sagebrush in association with *Conomyrma insana*.

Ten ants in one collection were taken from a burrow under a log in an association of grass, herbs, aspen, and pine. Ants of *Formica fusca* were in the same burrow. In 12 recorded Utah habitats it occurred six times in montane areas. In 8 elevation records between 4535 and 8000 ft it was most abundant under 6000, taken only twice above 6000.

Ponera pennsylvanica Buckley

P. pennsylvanica Buckley, 1866, Proc. Ent. Soc. Phila. 6:171; Smith 1979:1342.

Record: **COUNTY UNKNOWN**: locality unknown (Sm79).

Smith (1979:1342) lists this species from eastern to western United States, including Utah and Colorado, nesting under logs, stones, and other objects. Hunt and Snelling (1975:20) list it from Arizona. Gregg (1963:282) lists it between 3600 and 6970 ft under rocks in pinyon-juniper and cottonwood-willow habitats in Colorado.

Solenopsis aurea Wheeler

S. geminata var. *aurea* Wheeler, 1906, Amer. Mus. Nat. Hist., Bull. 22:336.

S. aurea: Ingham 1963:86.

Record: **WASHINGTON**: St George (I59).

Smith (1979:1385) lists this species from southwestern United States, including Arizona, in moundless nests in fully exposed situations. Cole (1966:17) found its nests in southern Nevada in open areas in blackbrush and hopsage-matrimony vine habitats. Ingham (1963) found it in Joshua trees and fourwing saltbush in southern Utah. Records for Utah range from 2500 to 3000 ft.

Solenopsis molesta (Say)

Myrmica molesta Say, 1836, Bost. J. Nat. Hist. 1:293.

S. molesta: Rees and Grundmann 1940:4; Cole 1942:361; Knowlton 1970:211, 1975:8.

S. molesta validiuscula: Cole 1942:361; Grundmann 1958:163; Ingham 1959:58; Beck et al. 1967:72; Knowlton 1970:211, 1975:8.

Records (Map 25): **BOX ELDER**: Cedar Crk (City), Kelton Pass, Snowville (K70), Wildcat Hills (US).

CACHE: Benson (C42), Cornish, Green Cyn (KU), Logan Cyn (C42), Millville, Paradise (KU). **CARBON**: Myton rd 15 and 22.7 mi E US6 (A). **DAVIS**: Kaysville (C42). **DUCHESNE**: Currant Crk (C42). **EMERY**: Greenriver (C42). **GARFIELD**: Carcass Crk (on Boulder Mt), Boulder (U). **GRAND**: Dewey (U), Moab (C42). **IRON**: Cedar City 7 mi E (I59). **JUAB**: Topaz Mt (KU). **KANE**: Kanab (C42), Long Valley (KU), Long Valley Jct 2 mi W (I59), Navajo Wells (BAD). **MILLARD**: White Valley (C42), Kanosh (US). **PIUTE**: Fish Lake Jct 1 mi S (U). **SALT LAKE**: Big Cottonwood Cyn (U), Emigration Cyn, Ft Douglas, Lake Blanche Trail, Little Willow Cyn, Parleys Cyn (C42), Salt Lake City (RG). **SAN JUAN**: Blanding, Bluff (G58), La Sal Crk (in La Sal Mts) (RG), Mexican Hat (G58). **SANPETE**: Ephraim Cyn (U). **TOOELE**: Ibapah (U), Iosepa, Orrs Ranch, Vernon Crk (C42), Rush Valley (BAD). **UINTAH**: Dry Fk rd 15 mi N U121 (A), Jensen (BAD), Paradise Park 11 mi S (U). **UTAH**: Diamond Fk Cyn (KU), Provo (C42), Spanish Fk Cyn, Wanrhodes Cyn (KU). **WASATCH**: Deer Crk Res, Midway (U), Soldier Summit (BAD) and 7.9 mi N (A). **WASHINGTON**: Beaver Dam Wash, Diamond Valley (BAD), Grafton (I59), Leeds (RG) and 5 mi N, New Harmony, Zion Nat Park (I59). **WAYNE**: Fruita 5 mi SE (U). **WEBER**: Ogden (C42).

Creighton (1950) lists two races of this species; the Utah one is likely *validiuscula*. Smith (1979:1387) lists this species distribution from Canada to eastern and western United States, but does not list an intermountain one. He indicates that it frequently nests in or near nests of other ants, from which it robs food and brood. Hunt and Snelling (1975:22) list it from Arizona. Gregg (1963:373, 375) lists it from Colorado between 3500 and 8378 ft under rocks in a variety of habitats. Cole (1966:17) found its nests in southern Nevada in pinyon-juniper and desert shrub habitats, frequently associated with *Pheidole pilifera*. He indicates that it nests under stones and logs or under bark, occasionally occupying the nests of other species in Utah (1942:361). In North Dakota Wheeler and Wheeler (1963) found it frequently under rocks. In Utah it is found under stones in brushy habitats and transition zones, common in desert conditions (Grundmann 1958:163). Ingham (1959, 1963) found it in southern Utah under stones, logs, and bark in pinyon-juniper, oak, sagebrush, rabbitbrush, squawbush, willow, tamarix, poplar, shadscale, and greasewood. Knowlton (1975:8) found it under stones in grass in northern Utah.

There were 247 ants in four collections taken from under rocks. Eggs were found under one rock and immature stages under another, both in early July. Ants of *Formica haemorrhoidalis* were found under the same rock in one instance, and *F. fusca* and *F. podzolica* in another. In both cases the colonies were separate. Three collections were in sagebrush: one in association with juniper; one grass, legumes, sagebrush, other shrubs, juniper, and pinyon; and one grass, aspen, and pine. One collection was in aspen and fir. In 65 recorded Utah habitats 16 were in montane forest. Of 42 recorded elevations between 2500 and 9000 ft the greatest number, 19, were between 4000 and 5000. Beck et al. (1967:72) found it feeding on dead rodents in seven instances in Utah.

Solenopsis salina Wheeler

S. salina Wheeler, 1908, Amer. Mus. Nat. Hist., Bull. 24:427; Ingham 1959:59.

Records: **WASHINGTON**: Kolob, Pine Valley (City) (I59).

Smith (1979:1388) lists this species from western United States, including Colorado, nesting under stones and wood. Hunt and Snelling (1975:22) list it from Arizona. Gregg (1963:378) lists it between 3500 and 7704 ft under rocks and wood in a variety of habitats in Colorado. Cole (1966:17) found it in southern Nevada under stones in pinyon-juniper. Ingham (1959) found it in southern Utah under stones in oak where it was associated with *Formica fusca*. Three Utah collections were taken between 6000 and 8000 ft.

Solenopsis xyloni McCook

S. xyloni McCook, 1879, (In) Comstock, Rpt. Cooton Ins., p. 188; Ingham 1959:58.

Records: **WASHINGTON**: Santa Clara (US), Shivwits Indian Res (I59), St George (US).

Smith (1979:1389) lists this species from eastern to western United States including Colorado, nesting in earthen mounds or under stones and other objects. Hunt and Snelling (1975:22) list it from Arizona. Gregg (1963:373) lists it at 4400 ft under rocks in cottonwood-willow and grassy habitats in Colorado. Cole (1966:17) found its nests in southern Nevada at the base of shrubs in creosote bush habitats. Ingham (1959) found it under rocks in creosote bush, poplar, willow, datura, and rabbitbrush in southern Utah. Known habitats in Utah are in desert areas.

Stenamma brevicorne (Mayr)

Aphaenogaster brevicornis Mayr, 1886, Verh. Zool.-Bot. Ges. Wien 36:443.

S. brevicorne: Cole 1942:363; Knowlton 1975:8.

Record: **BOX ELDER**: Snowville 17 mi SW (KU). **CACHE**: Logan (C42).

Smith (1979:1358) lists this species from eastern to western United States, including Colorado, nesting under stones or wood in wooded areas. Gregg (1963:348) lists it at 3800 ft in deciduous areas in Colorado. Knowlton (1975:8) found it associated with sagebrush and shadscale in northern Utah.

Stenamma chiricahua Snelling

S. chiricahua Snelling, 1973, Los Angeles Co. Mus., Contr. Sci. 245:7.

Record: **MORGAN**: Morgan (KU).

Smith (1979:1358) lists this species from mountains in southern Arizona. Its occurrence in Utah is questionable.

Stenamma diecki Emery

S. westwoodi diecki Emery, 1895, Zool. Jahrb. Syst. 8:300.

S. diecki: Cole 1942:363; Smith 1957:140; Snelling 1973:18; Knowlton 1975:8.

Records (Map 25): **BOX ELDER**: Cedar Hill, Wildcat Hills (K75). **CACHE**: Blacksmith Fk Cyn, Green Cyn (KU), Logan (C42), Logan Cyn, Trenton (KU). **UTAH**: American Fk Cyn (U).

Smith (1979:1358) lists this species from eastern to western United States, but does not indicate an intermountain state. It nests under wood or other objects in wooded areas. Wheeler and Wheeler (1978:391) found it at 6400 ft in Nevada, and frequently under and in wood in North Dakota (1963). Gregg (1963:350) lists it from Colorado between 6050 and 7350 ft under rocks in conifers. In eight recorded Utah habitats it was taken four times in montane forest. Three recorded elevations were between 4460 and 7000 ft.

Stenamma huachucanum M.R. Smith

S. huachucanum Smith, 1957, Amer. Midl. Nat. 57:153; Knowlton 1975:8.

Records: **BOX ELDER**: Hansel Mts, Hardup, Kelton Pass, Snowville (K75).

Smith (1979:1359) lists this species only from Arizona nesting under rocks. Gregg (1963:350) lists it from Colorado at 8300 ft under rocks in mixed forest. Knowlton (1975:8) found it associated with sagebrush, rabbitbrush, and junipers in northern Utah.

Stenamma impar Forel

S. brevicorne impar Forel, 1901, Soc. Ent. de Belg., Ann. 45:347.

Record: **UTAH**: Spanish Fk Cyn (KU).

Smith (1979:1359) lists this species as eastern to midwestern United States, and does not indicate an intermountain state. It nests in soil or rotten wood.

Stenamma occidentale M.R. Smith

S. occidentale Smith, 1957, Amer. Midl. Nat. 57:146; Snelling 1973:25; Smith 1979:1359.

Records (Map 25): **CACHE**: Blacksmith Fk Cyn, Green Cyn, Leeds Cyn, Paradise (KU). **UINTAH**: Bonanza (KU). **UTAH**: Diamond Fk Cyn (KU).

Smith (1979:1359) lists this species from midwest and western United States, including Utah, Colorado, Arizona, and Idaho, nesting under rocks. Gregg (1963:353) lists it from Colorado between 5900 and 8500 ft under rocks in conifers, birch, and oak habitats.

Stenamma smithi Cole

S. smithi Cole, 1966, Brigham Young U. Sci. Bull. 7(3):7; Knowlton 1975:9; Smith 1979:1359.

S. knowltoni: Gregg 1972:35; Knowlton 1975:8.

Records (Map 26): **BOX ELDER**: Cedar Crk Jct (Gr), Cedar Hill (US), Curlew Valley Jct, Hansel Mts, Hardup, Kelton Pass, Snowville (K75). **CACHE**: Newton (KU).

Smith (1979:1359) lists this species from Utah, Nevada, and Idaho, nesting in sagebrush and juniper duff. Cole (1966:8) found the type series in mixed brush in Nevada. Gregg (1972:38) lists its Colorado habitats as duff of sagebrush, juniper, and greasewood, and in grass. Wheeler and Wheeler (1978:391) found it at 7000 ft in Nevada. Knowlton (1975:8, 9) found it associated with sagebrush, grass, greasewood, and rabbitbrush in northern Utah.

Tapinoma sessile (Say)

Formica sessile Say, 1836, Bost. J. Nat. Hist. 1:287.

T. sessile: Rees and Grundmann 1940:6; Cole 1942:372; Hayward 1945:120; Grundmann 1958:165; Ingham 1959:68; Beck et al. 1967:73; Knowlton 1970:212, 1975:9.

Records (Map 26): **BOX ELDER**: Bear River City (US), Brigham 0.9 mi E (A), Cedar Crk (City) (K70), Cedar Hill (K75), Hansel Mts, Kelton Pass (K70), Locomotive Spngs (BAD), Mantua (KU), Raft River S Fk (RG), Snowville (K75), Taylor Farms (K70), Wildcat Hills (K75). **CACHE**: Ant Valley, Blacksmith Fk Cyn (KU), Cowley Cyn (C42), Green Cyn, Leeds Cyn (KU), Logan, Logan Cyn (C42), Mendon Cold Spng, Providence, Tony Grove (KU). **CARBON**: Jct Soldier Summit rd and U33 1.7 mi W (A). **DAGGETT**: Radosovich Ranch (BAD). **DAVIS**: Antelope Island (US), Farmington (C42). **DUCHESNE**: Fruitland 5 mi E (US), Johnny Star Flat (BAD), Tabiona 11.6 mi E (A). **EMERY**: Greenriver (US). **GARFIELD**: Boulder Mt, Henry Mts (G58). **IRON**: Enoch (BAD), Modena 10.4 mi NE (A), Newcastle 1 mi E (159). **JUAB**: Nephi (US). **KANE**: Kanab (C42), Long Valley Jct (159). **MILLARD**: White Valley (C42). **MORGAN**: Morgan (KU). **SALT LAKE**: Arthur (US), Big Cottonwood Cyn, Draper (C42). **SAN JUAN**: Abajo Mts, Blanding, Bluff (G58), Hole-in-the-Rock Cyn (U), Kigalia Ranger Sta (BAD), Monticello 7.6 mi W (A). **SEVIER**: Monroe (US). **SUMMIT**: Echo (BAD), Kamas 14.7 mi E, Mirror Lake 17.3 mi N (A). **UINTAH**: Bonanza (KU), Dry Fk rd 13.4 mi N U121, Red Cloud Loop rd 4.2 mi W U44 (A). **UTAH**: Payson Cyn 12.3 mi up (A), Provo (BAD), Thistle 7.7 mi E (A). **WASATCH**: Hanna 9.2 mi W, Soldier Summit 3.3 and 10.1 mi N (A), Strawberry Valley (US), Strawberry Res 4 mi S (A). **WASHINGTON**: Leeds (RG), Pine Valley (City), Santa Clara (159), Toquerville (BAD), Zion Nat Park (159). **WAYNE**: Hanksville (BAD).

Smith (1979:1421) lists this as primarily an eastern species (no intermountain state is listed) that nests mostly under objects in a variety of habitats. Hunt and Snelling (1975:22) list it from Arizona. Gregg (1963:446) lists it from Colorado between 3500 and 10,505 ft under rocks and wood in a variety of habitats, predominantly in conifers. La Rivers (1968:7) lists it from Nevada, where Wheeler and Wheeler (1978:392) found it between 6100 and 10,500 ft. They found it frequently under rocks, also common in wood in North Dakota (1963). Allred and Cole (1971:239) found it in Idaho in associations of wild rye-grass and rabbitbrush-sagebrush-grass-winterfat. Cole (1942:372) indicates that in Utah it nests under stones, logs, and bark. Grundmann (1958:165) indicates that it is common in Utah in mountain brush in large nests usually under stones in shady areas between 4000 and 8000 ft. Ingham (1959, 1963) found it in southern Utah under rocks, logs, and in grass clumps in a variety of vegetative types. Knowlton (1975:9) found it associated with sagebrush, shadscale, greasewood, snowberry, and rabbitbrush in northern Utah.

There were 556 ants in 13 collections taken from under rocks. In one instance *Lasius alienus* was under the same rock. Eighty ants in 3 collections were taken from under logs. Thirty ants in one collection were taken from a small mound, and 20 in one collection singly in an open area. Immatures were found under two rocks in mid-July and under a log in late June. Fourteen collections were taken in sagebrush: 3 in association with grass, 2 snowberry, 2 matchbrush, one grass and herbs, one legumes, and one aspen and conifers. One collection was in a herb meadow with aspen; one grass, herbs, shrubs, and aspen; one herbs, sedges, and conifers; and one grass, herbs, aspen, and conifers. In 70 recorded Utah localities 26 were in montane areas. At 31 recorded elevations between 2500 and 8402 ft, 22 were between 4000 and 6000. Beck et al. (1967:73) found it feeding on dead rodents in 12 instances in Utah.

Tetramorium caespitum (Linnaeus)

Formica caespitum Linnaeus, 1758, 10th ed. Syst. Nat. 1:581.

Record: **SALT LAKE**: Salt Lake City (KU).

Smith (1979:1400) lists this species from eastern to western United States, including Nevada, nesting in a variety of situations.

Veromessor lobognathus (Andrews)

Messor lobognathus Andrews, 1916, Psyche 23(3):82.

V. lobognathus: Wheeler and Wheeler 1967:240; Allred and Cole 1979:99.

Records: **DUCHESNE**: Duchesne 11 mi W (W67). **KANE**: Glen Cyn City (AC).

Smith (1979:1364) lists this species from midwest to western United States, including Colorado and Nevada, nesting under stones. Gregg (1963:354) lists it between 5747 and 6500 ft under rocks in pinyon-juniper and sagebrush areas. Cole (1966:12) found it a common species in pinyon-juniper in southern Nevada, nesting under large rocks. Allred and Cole (1979:99, 1971:239) found it in southern Utah and Idaho in various associations of desert shrubs. It was most abundant in rabbitbrush-sagebrush. Wheeler and Wheeler (1963) found it frequently under rocks in North Dakota, and indicate that it is rarely taken, occurs between 7000 ft in the southern part of its range to 2500 ft at the northern part, and is an inhabitant of pinyon-juniper, where it nests under stones (1965:60). They found a nest in Utah under a mound of earth at the base of a clump of grass in an association of sagebrush, saltbush, and grass (1967:240).

Synonymies and Corrections of Utah Records

Names on the left are as written in published literature or on labels on specimens in collections I examined (many representing heretofore unpublished data), and for purposes of this paper are considered to be errors in identification unless other authors have treated them as junior synonyms to the names on the right.

- Acanthomyops
  - claviger = A. interjectus
  - coloradensis = A. interjectus
- Aphaenogaster
  - subterranea valida = A. occidentalis
- Brachymyrmex
  - depilis flavescens = B. depilis
- Camponotus
  - caryae decipiens = C. nearcticus
  - herculeanus ligniperda noveboracensis = C. novaeboracensis
  - herculeanus pennsylvanicus = C. herculeanus
  - herculeanus whymperi = C. herculeanus
  - ligniperdus noveboracensis = C. novaeboracensis
  - maccooki = C. semitestaceus
  - maculatus sansabeanus = C. sansabeanus
  - maculatus sansabeanus torrefactus = C. sansabeanus
  - maculatus vicinus = C. vicinus
  - marginatus nearcticus = C. nearcticus
  - nearcticus decipiens = C. nearcticus
  - pennsylvanicus = C. modoc
  - pennsylvanicus modoc = C. modoc
  - sansabeanus sansabeanus = C. sansabeanus
  - sansabeanus torrefactus = C. sansabeanus
  - sansabeanus vicinus = C. vicinus
  - sansabeanus vicinus luteangulus = C. vicinus
  - sansabeanus vicinus nitidiventris = C. vicinus
  - sylvaticus maccooki = C. semitestaceus
- Crematogaster
  - coarctata mormonum = C. mormonum
  - lineolata = C. emeryana
  - lineolata cerasi = C. emeryana
  - lineolata coarctata = C. mormonum
  - lineolata coarctata mormonum = C. mormonum
  - lineolata emeryana = C. emeryana
  - lineolata opaca depilis = C. depilis
  - punctulata = C. emeryana
  - vermiculata = C. coarctata
- Dorymyrmex = Conomyrma
  - bicolor = C. bicolor
  - pyramicus = C. insana
  - pyramicus bicolor = C. bicolor
  - pyramicus flavus = C. insana
  - pyramicus pyramicus = C. insana
- Eciton = Neivamyrmex
  - sp. = probably N. californicus
- Formica
  - aliena = Lasius alienus
  - cinerea = F. canadensis
  - cinerea altipetens = F. altipetens
  - cinerea canadensis = F. canadensis
  - cinerea cinerea altipetens = F. altipetens
  - cinerea lepida = F. canadensis
  - cinerea neocinerea = F. canadensis
  - claviger = Acanthomyops claviger
  - crinata = F. criniventris
  - crinoventris = F. criniventris
  - flava = Lasius nearcticus
  - foreliana = F. gnava
  - fusca argentata = F. argentea
  - fusca argentea = F. argentea
  - fusca cinerea = F. altipetens
  - fusca densiventris = F. densiventris
  - fusca gelida = F. neorufibarbis
  - fusca neoclara = F. neoclara
  - fusca neorufibarbis = F. neorufibarbis
  - fusca pruinosa = F. neoclara
  - fusca subaenescens = F. fusca
  - fusca subpolita = F. subpolita
  - fusca subpolita neogagates = F. neogagates
  - fusca subpolita perpilosa = F. perpilosa
  - fusca subsericea = F. fusca
  - herculeana = Camponotus herculeanus
  - insana = Conomyrma insana
  - integra = F. haemorrhoidalis
  - integra haemorrhoidalis = F. haemorrhoidalis
  - integroides coloradensis = F. integroides
  - integroides propinqua = F. integroides
  - integroides planipilis = F. integroides
  - laevigatus = Camponotus laevigatus
  - latipes = Acanthomyops latipes
  - marcida = F. fusca
  - microgyna = F. rasilis
  - microgyna rasilis = F. rasilis
  - moki = F. xerophila
  - moki grundmanni = F. xerophila
  - moki xerophila = F. xerophila
  - montana = F. canadensis
  - neogagates lasioides vetula = F. lasioides
  - neorufibarbis gelida = F. neorufibarbis
  - niger = Lasius niger
  - novoboracensis = Camponotus novaeboracensis
  - obscuriventris clivia = F. obscuriventris
  - oreas comptula = F. oreas
  - oreas oreas = F. oreas
  - pallidefulva nitidiventris = F. pallidefulva
  - pallidefulva nitiventris = F. pallidefulva
  - pennsylvanica = Camponotus modoc
  - planipilis = F. integroides
  - propinqua = F. integroides
  - pruinosa = F. neoclara
  - rasilis spicata = F. densiventris
  - rufa aggerans = F. obscuripes
  - rufa clivia = F. obscuriventris
  - rufa coloradensis = F. integroides
  - rufa haemorrhoidalis = F. haemorrhoidalis
  - rufa laeviceps = F. laeviceps
  - rufa melanotica = F. obscuripes
  - rufa muscescens = F. mucescens
  - rufa obscuripes = F. obscuripes
  - rufa obscuriventris integroides = F. integroides

rufibarbis gnava = F. gnava
rufibarbis occidua = F. occidua
sanguinea = F. subnuda
sanguinea obtusopilosa = F. obtusopilosa
sanguinea puberula = F. puberula
sanguinea rubicunda subnuda = F. subnuda
sanguinea subnuda = F. subnuda
sansabeanus = Camponotus sansabeanus
sessilis = Tapinoma sessile
subaenescens = F. subnitens
subpolita camponoticeps = F. subpolita
subpolita ficticia = F. subpolita
subsericea = F. fusca
truncicola integroides = F. integroides
truncicola integroides coloradensis = F. integroides
truncicola integroides haemorrhoidalis = F. haemorrhoidalis
truncicola mucescens = F. mucescens
truncicola obscuriventris = F. obscuriventris
truncicola obscuriventris aggerans = F. obscuriventris
umbrata = Lasius umbratus
vinculans = F. neogagates
whymperi alpina = F. whymperi

Iridomyrmex
analis = I. pruinosus
pruinosus analis = I. pruinosus
pruinosus pruinosus = I. pruinosus
pruinosus testaceus = I. pruinosus

Lasius
alienus americanus = L. alienus
americanus = L. niger
americanus sitkaensis = L. pallitarsus
claviger = Acanthomyops coloradensis
flavus = L. nearcticus
flavus claripennis = L. nearcticus
flavus microps = L. nearcticus
flavus nearcticus = L. nearcticus
interjectus = Acanthomyops interjectus
latipes = Acanthomyops latipes
murphyi = Acanthomyops murphyi
neoniger = L. niger
niger alienus americanus = L. alienus
niger americanus = L. alienus
niger neoniger = L. niger
niger sitkaensis = L. pallitarsus
pilosus = L. vestitus
sitkaensis = L. pallitarsus
umbratus aphidicola = L. umbratus
umbratus mixtus aphidicola = L. umbratus
umbratus subumbratus = L. subumbratus

Leptothorax
acervorum canadensis = L. muscorum
acervorum canadensis yankee = L. muscorum
acervorum crassipilis = L. crassipilis
canadensis = L. muscorum
canadensis yankee = L. muscorum
nevadensis nevadensis = L. nevadensis
pilifera = Pheidole pilifera
rugatulus brunnescens = L. rugatulus
rugatulus rugatulus = L. rugatulus
sitkaensis = Lasius pallitarsus
tricarinatus tricarinatus = L. tricarinatus
tricarinatus neomexicanus = L. tricarinatus

Liometopum
apiculatum luctuosum = L. occidentale
luctuosum = L. occidentale
microcephalum occidentale = L. occidentale
occidentale luctuosum = L. occidentale
tricarinatus = L. occidentale

Myrmecocystus
melliger = M. mendax
melliger mendax = M. mendax
melliger orbiceps = M. mendax
melliger semirufus = M. kennedyi
mexicanus hortideorum = M. mexicanus
mexicanus mojave = M. testaceus
mexicanus navajo = M. navajo
mojave = M. testaceous

Myrmica
brevinodis = M. incompleta
brevinodes brevispinosa = M. brevispinosa
brevinodes discontinua = M. brevispinosa
brevinodis sulcinodoides = M. incompleta
californica = Pogonomyrmex californicus
emeryana emeryana = M. emeryana
emeryana tahoensis = M. emeryana
fracticornis = M. lobicornis
hamulata hamulata = M. hamulata
hunteri = Manica hunteri
incompleta incompleta = M. incompleta
lineolata = Crematogaster emeryana
lobicornis fracticornis = M. lobicornis
lobicornis lobifrons = M. lobicornis
lobifrons = M. lobicornis
mojave = M. testaceus
molesta = Solenopsis molesta
mutica = Manica mutica
occidentalis = Pogonomyrmex occidentalis
rubra brevinodis = M. incompleta
rubra brevinodis brevispinosa = M. brevispinosa
rubra brevinodis sulcinodoides = M. incompleta
rubra scabrinodis fracticornis = M. lobicornis
sabuleti americana = M. americana
sabuleti hamulata = M. hamulata
scabrinodis = M. monticola
scabrinodis brevinodis = M. emeryana
scabrinodis lobocornis fracticornis = M. lobicornis
scabrinodis mexicana = M. emeryana
scabrinodis schenki emeryana = M. emeryana
scabrinodis schenki monticola = M. monticola
scabrinodis sulcinodoides = M. emeryana
schenecki emeryana = M. emeryana

Novomessor
albisetosus = Aphaenogaster uinta

Pheidole
bicarinata buccalis = P. bicarinata
bicarinata longula = P. bicarinata
bicarinata vinelandica = P. bicarinata
bicarinata paiute = P. bicarinata
californica oregonica = P. californica
longula = P. bicarinata
morrisi dentata = P. dentata
pilifera artemisia = P. pilifera
pilifera coloradensis = P. pilifera
pilifera pilifera = P. pilifera
sitarches sitarches = P. sitarches
sitarches soritis = P. sitarches
soritis = P. sitarches

Pogonomyrmex
barbatus fuscatus = P. barbatus
barbatus marfensis = P. barbatus
barbatus molefaciens = P. barbatus
barbatus rugosus = P. rugosus
californicus maricopa = P. maricopa
occidentalis comanche = P. occidentalis
occidentalis occidentalis = P. occidentalis
occidentalis owyheei = P. owyheei
occidentalis subnitidus = P. subnitidus
occidentalis utahensis = P. occidentalis
Polygerus
rufescens = P. breviceps
rufescens breviceps = P. breviceps
rufescens fusca subumbratus = P. breviceps
rufescens umbratus = P. breviceps
Ponera
coarctata pennsylvanica = P. pennsylvanica
opaciceps = Hypoponera opaciceps
trigona = P. pennsylvanica
trigona opacior = Hypoponera opacior
Solenopsis
molesta validiuscula = S. molesta
Stenamma
knowltoni = S. smithi
Symmyrmica
chamberlini = Formicoxenus chamberlini
Tapinoma
pruinosum = Iridomyrmex pruinosus

Literature Cited

Allred, D. M. 1980. Swarming of the western harvester ant, *Pogonomyrmex occidentalis*. Great Basin Nat. 40(2):165–6.

Allred, D. M., and A. C. Cole. 1971. Ants of the National Reactor Testing Station. Great Basin Nat. 31(4):237–42.

______. 1979. Ants from northern Arizona and southern Utah. Great Basin Nat. 39(1):97–102.

Beck, D E., D. M. Allred, and W. J. Despain. 1967. Predaceous-scavenger ants in Utah. Great Basin Nat. 27(2):67–78.

Bohart, G. E., and G. F. Knowlton. 1953. Notes on the food habits of the western harvester ant. Proc. Ent. Soc. Washington 55(3):151–3.

Buren, W. F. 1968. Review of the species of *Crematogaster* in North America. J. Georgia Ent. Soc. 3(3):91–121.

Clark, W. H., and N. P. Yensen. 1976. The ants of Idaho. Bull. Oregon Ent. Soc. 61:501.

Cole, A. C. 1942. The ants of Utah. Amer. Midl. Nat. 28(2):358–88.

______. 1953. *Brachymyrmex depilis* subsp. *flavescens* Grundmann a synonym of *Brachymyrmex depilis* Emery. Ent. News 64(10):266.

______. 1955. Studies of New Mexico ants. XV. Additions, corrections, and new synonymy. J. Tennessee Acad. Sci. 30(1):49–50.

______. 1956. Observations of some members of the genus *Pheidole* in the southwestern United States with synonymy. J. Tennessee Acad. Sci. 31(2):112–18.

______. 1957. Notes on western ants. J. New York Ent. Soc. 65:129–31.

______. 1966. Ants of the Nevada Test Site. BYU Sci. Bull. Biol. Ser. 7(3):1–27.

______. 1968. *Pogonomyrmex* harvester ants: a study of the genus in North America. Univ. of Tennessee Press, Knoxville, 222 pp.

Creighton, W. S. 1950. The ants of North America. Bull. Mus. Comp. Zool. 104:1–585.

Cresson, E. T. 1874. Report on collections of Hymenoptera made in portions of Nevada, Utah, Colorado, New Mexico, and Arizona during the years 1872–1874. Geogr. Explor. West of 100th Meridian, Washington, D.C., 1875:705–36.

Francoeur, A. 1973. Revision taxonomique des especes Nearctiques du Groupe *fusca*, genre *Formica* (Formicidae, Hymenoptera). Mem. Soc. Entomol. Quebec, Mem. 3, 316 pp.

______. 1974. Notes for a revision of the ant genus *Formica*. 1. New identifications and synonymies for some Nearctic specimens from Emery, Forel and Mayr collections. Ent. News 85(9 & 10):257–64.

Garrett, A. O. 1910. Honey ants in Utah. Science 32:342–3.

Gregg, R. E. 1963. The ants of Colorado. Univ. Colorado Press, Boulder, Colo. 792 pp.

______. 1972. A new species of *Stenamma* from Utah. Great Basin Nat. 32(1):35–9.

Grundmann, A. W. 1939. The ants of Salt Lake County (with a list of the known ants of Utah). Unpublished thesis. Univ. of Utah.

______. 1952. A new *Brachymyrmex* from northern Utah. J. Kansas Ent. Soc. 25:117.

______. 1958. Ants. Pages 161–167 *in* Preliminary report on biological resources of the Glen Canyon Reservoir. Univ. Utah Anthr. Papers, No. 31.

Hayward, C. L. 1945. Biotic communities of the southern Wasatch and Uinta mountains, Utah. Great Basin Nat. 6(1–4):1–124.

Hunt, J. H., and R. R. Snelling. 1975. A checklist of the ants of Arizona. J. Arizona Acad. Sci. 10(1):20–3.

Ingham, C. D. 1959. Ants of the Virgin River Basin, southwestern Utah. Unpublished thesis. Univ. of Utah. 140 pp.

______. 1963. An ecological and taxonomic study of the ants of the Great Basin and Mohave Desert regions of southwestern Utah. Unpublished dissertation. Univ. of Utah. 212 pp.

James, F. K. 1950. The ants of Red Butte Canyon. Unpublished thesis. Univ. of Utah.

Knowlton, G. F. 1946. Birds feeding on ants in Utah. J. Econ. Ent. 39:547–8.

______. 1963. Western harvester ant control for Utah. Utah State Univ. Ext. Leafl. 48(Rev.), p. 1.

______. 1970. Ants of Curlew Valley. Proc. Utah Acad. Sci., Arts and Letters 47(1):208–12.

______. 1975. Ants of Curlew Valley, Utah and Idaho. Utah State Univ. Ecol. Ctr., Terr. Arth. Ser. 13, 10 pp.

Knowlton, G. F., and W. P. Nye. 1946. Lizards feeding on ants in Utah. J. Econ. Ent. 39(4):546–7.

La Rivers, I. 1968. A first listing of the ants of Nevada. Biol. Soc. Nevada, Occ. Papers, 12 pp.

Olsen, O. W. 1934. Notes on the North American harvesting ants of the genus *Pogonomyrmex* Mayr. Bull. Mus. Comp. Zool. 77(8):493–514.

REES, D. M., AND A. W. GRUNDMANN. 1940. A preliminary list of the ants of Utah. Bull. Univ. Utah 31(5):1-12.

SMITH, D. R. 1979. Family Formicidae. Pages 1323-1467 *in* Catalogue of Hymenoptera in America North of Mexico. Smithsonian Inst. Press, Wash., D.C.

SMITH, M. R. 1952. North American *Leptothorax* of the *tricarinatus-texanus* complex. J. New York Ent. Soc. 50:96-106.

______. 1953. A new *Pheidole* (subgenus *Ceratopheidole*) from Utah. J. New York Ent. Soc. 61:143-6.

______. 1957. Revision of the genus *Stenamma* Westwood in America north of Mexico. Amer. Midl. Nat. 57:133-74.

SNELLING, R. R. 1970. Studies on California ants, 5. Revisionary notes on some species of *Camponotus*, subgenus *Tanaemyrmex*. Proc. Ent. Soc. Washington 72(3):390-7.

______. 1973-a. The ant genus *Conomyrma* in the United States. Los Angeles County Nat. Hist. Mus., Contr. 238, 6 pp.

______. 1973-b. Studies on California ants, 7. The genus *Stenamma*. Los Angeles County Nat. Hist. Mus., Contr. 245, 38 pp.

______. 1976. A revision of the honey ants, genus *Myrmecocystus*. Los Angeles County Mus. Nat. Hist., Sci. Bull. 24, 163 pp.

WEBER, N. A. 1947. A revision of the North American ants of the genus *Myrmica*. Ann. Ent. Soc. Amer. 40:437-47.

WHEELER, G. C., AND J. WHEELER. 1963. The ants of North Dakota. Univ. of North Dakota Press. Grand Forks. 326 pp.

______. 1965. *Veromessor lobognathus*: third note. J. Kansas Ent. Soc. 38(1):55-61.

______. 1967. *Veromessor lobognathus*: fourth note. J. Kansas Ent. Soc. 40(2):238-41.

______. 1970. The natural history of *Manica*. J. Kansas Ent. Soc. 43(2):129-62.

______. 1977. North Dakota ants updated. Desert Res. Inst. Publ., Reno, Nevada. 27 pp.

______. 1978. Mountain ants of Nevada. Great Basin Nat. 38(4):379-96.

WHEELER, W. M. 1904. Three new genera of inquiline ants from Utah and Colorado. Bull. Amer. Mus. Nat. Hist. 20:1-17.

WILSON, E. O. 1955. A monographic revision of the ant genus *Lasius*. Bull. Mus. Comp. Zool. 113(1):1-205.

WING, M. W. 1968. Taxonomic revision of the nearctic genus *Acanthomyops*. Cornell Univ. Agric. Expt. Sta., Mem. 405. 173 pp.

WOODBURY, A. M. 1952. Gazetteer of Utah localities and altitudes. Div. Biol., Univ. of Utah. Salt Lake City. 216 pp.

VEGETAL RESPONSES AND BIG GAME VALUES AFTER THINNING REGENERATING LODGEPOLE PINE[1]

D. D. Austin[2] and Philip J. Urness[2]

Abstract.— Understory vegetal response was found to significantly increase with the degree of thinning in an early regenerating, dense stand of lodgepole pine (*Pinus contorta*). The value of the increased vegetation for deer and elk was determined to be important through comparisons with known dietary and habitat preferences.

Following removal of mature lodgepole pine stands, regeneration is frequently dense and results in early stagnation (Forest Service 1962). Although thinning of young stands often increases the rate of growth (Trappe 1959) and harvested yields (Wikstrom and Wellner 1961), other values should be considered, especially when cost/benefit ratios for timber are marginal. Increases in forage production are a potential additional value; however, the relationship between forest thinning and big game habitat values remains ambiguous (Wallmo and Schoen 1981:445). This paper reports the response of understory vegetation four years following thinning treatments in a dense, 16-year-old lodgepole pine stand and, using previously determined diets and habitat preferences, assesses the potential value for deer and elk.

Area and Methods

The study was on the Ashley National Forest in northeastern Utah near East Park Reservoir at 2700 m elevation. Lodgepole pine covers 92 percent of the area, which is an undulating upland draining to the south.

Natural regeneration of forest stands following harvest or fire in the area has resulted in dense stands of trees, usually requiring thinning to prevent stand stagnation. This study was conducted on one such stand bulldozed and broadcast burned for wildlife and timber values in 1960 and 1961. The regenerated stand in 1976 had a density of 6200 stems per ha and mean height of 2 m compared to the adjacent untreated stand with about 8500 stems per ha and 10 m height.

Three replicates of four macroplots, each 20 × 20 m with 4 m buffer strips, were arranged in a randomized block design. Clearcut, heavy thinning, moderate thinning, and control treatments were established during August 1976 (Fig. 1); trees were handcut and removed. The heavy and moderate thinning treatments left about 1100 and 2200 stems per ha, respectively, which compare with about 1300 stems per ha in nearby stands scheduled for logging and 2000 stems per ha for estimated maximum yield in the Rocky Mountains (Forest Service 1962). Vegetal production and ground cover were determined during August 1976 and 1980 using the microplot-macroplot approach (Poulton and Tisdale 1960) with the modifications of Deschamp et al. (1979). Estimates were recorded on each of 40 microplots (20 × 50 cm) within each macroplot, with every tenth plot subsequently clipped and weighed for double sampling regression analysis. The 1980 data were subjected to a covariance analysis using 1976 as the covariant.

Vegetal Change

The response of understory vegetation to tree removal was determined using four indices (Table 1). The first two indices, production and ground cover, indicate the amount of vegetal change, and the latter two, density

---

[1] This study was partially supported by funds from the Pittman-Robertson Act under Utah Division of Wildlife Resources Project W-105-R.

[2] Department of Range Science, Utah State University, Logan, Utah 84322.

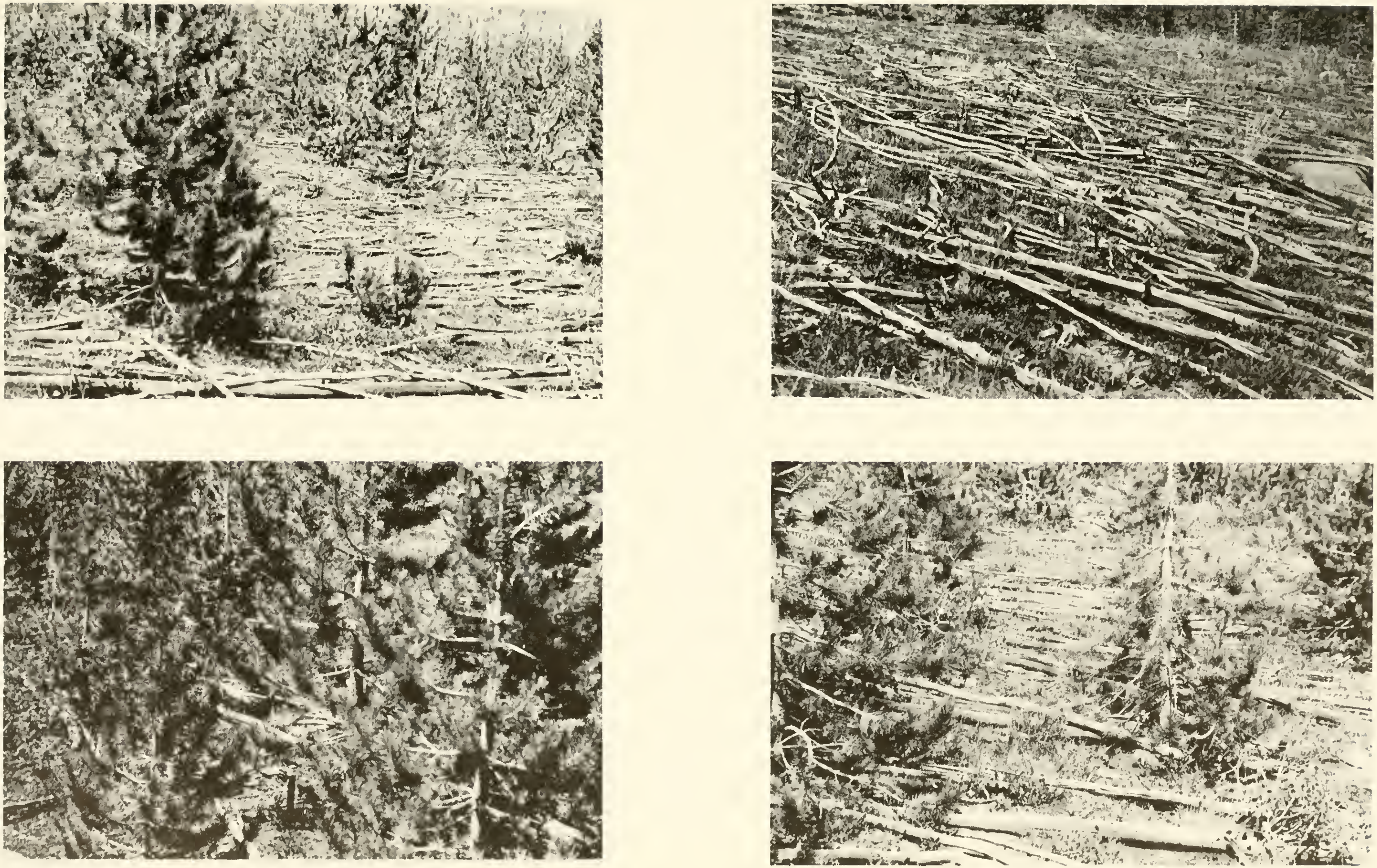


Fig. 1. Stand reduction treatments on lodgepole pine regenerating forests: clearcut (upper left), heavy thinning (upper right), moderate thinning (lower left), and control (lower right).

and number of species, reflect community complexity. With the four indices the mean response between 1976 and 1980 was generally greatest in the clearcut, followed by the heavy thinning, moderate thinning, and control.

Mean understory production increased 82 percent on the clearcut, 8 percent on the heavy thinning, 2 percent on the moderate thinning, and the control decreased 18 percent. Ground cover increased a mean 102 percent on the clearcut, 47 percent on the heavy thinning, 17 percent on the moderate thinning, and 14 percent on the control. The differences in production and cover due to treatment effects were significant ($p < .05$).

Species density, the mean number of species encountered on the 0.1 m^2 plots, and the number of species present per macroplot showed similar trends. Density increased 59, 43, 26, and 16 percent on the clearcut, heavy thinning, moderate thinning, and control, respectively, and the mean number of species increased 5.4 on the clearcut and heavy thinning, 4.0 on the moderate thinning, and 1.6 on the control. However, responses due to treatment effects were not significant, although species density approached significance ($P < .06$).

Means adjusted for pretreatment condition showed significant differences between treatments (Table 1). The adjusted means represent the expected values in the fourth year following treatments that would have resulted had initial data on all macroplots within replications been equal. The clearcut treatment showed significant increases ($P < .05$) in indices' values over those of the control in production, cover, and density, with number of species approaching significance ($P < .08$). Similarly, the heavy treatment was significant in cover, density, and number of species, and production approached significance ($P < .07$). None of the values in the moderate thinning were significant ($P < .05$); production became significant at $P < .10$ and number of species at $P < .09$, however.

These results show a substantial increase in the amount of understory forage and plant community complexity following clearcut and heavy thinning treatments. Furthermore, although the control showed a decrease in production and only a slight increase in cover, density, and number of species, the clearcut and heavy thinning treatments, in contrast, showed a positive change in production and much larger increases in the other indices. The moderate treatment had lesser increases. Although each of the four indices evaluated in this study is useful in describing community composition, it is apparent that production and cover are more sensitive in detecting changes. Similar results have been reported by Basile and Jensen (1971) and Regelin et al. (1974) in clearcut areas of lodgepole pine forests elsewhere.

VALUE TO BIG GAME

Although a treatment may result in significant increases in plant production, unless the increase is within preferred grazing areas and composed of species palatable to potential grazers, changes in forage production are inconsequential. Of the five major vegetal segments within the study area—wet and dry meadow and mature, stagnated, and regen-

TABLE 1. Mean indices of understory vegetal changes: production (kg/ha), ground cover (%), species density (species/0.1 m^2), and number of species (species/macroplot).

	Production	Cover	Density	Number
Treatment	1976–1980	1976–1980	1976–1980	1976–1980
Clearcut	181–329	21–43	2.8–4.4	13–19
Heavy thinning	195–210	20–30	2.5–3.6	11–17
Moderate thinning	172–176	20–24	2.7–3.3	9–13
Control	180–147	19–21	2.3–2.7	10–11
Clearcut	330^{a}	41^{a}	4.2^{a}	16^{ac}
Heavy thinning	196^{b}	30^{b}	3.7^{ab}	16^{ab}
Moderate thinning	187^{b}	23^{bc}	3.3^{bc}	15^{ac}
Control	149^{b}	23^{c}	2.9^{c}	13^{c}

[a,b,c]Different letters are Adjusted Means and indicate significance at $p < .05$ within columns.

erating lodgepole pine forest—regenerating lodgepole pine was the most preferred habitat for deer (Deschamp et al. 1979), and it was second only to the wet meadow for elk (Collins et al. 1978). Thus, increases in production due to thinning would occur in habitats favored by big game.

Potential forage benefits were assessed by comparing the 1976 and 1980 production data of major species (Table 2) with the corresponding dietary preferences for deer (Deschamp 1977) and elk (Collins 1977). Forage preferences were obtained from the ratio of percent diet composition to percent available production (Neff 1974); and preference categories (Table 2), although arbitrarily determined, corresponded to animal selection of forage species under free-ranging field conditions. In response to thinning, most forb species increased in production or remained about the same. Production of grass and sedge species also increased in production except short-stemmed sedge (*Carex brevipes*), which decreased. Conversely, production of browse species tended to show little response to treatment.

Generally deer and elk showed a preference for most browse and forb species, and grasses and sedges were rejected (Table 2). Consequently, the increased production of grasses and sedges would have little benefit to big game. Production increases in forbs could be highly beneficial, particularly since forbs comprised the large majority of the diets; deer 94 percent (Deschamp et al. 1979) and elk 86 percent (Collins et al. 1978). The small response of browse species would not likely affect the diet.

In densely forested areas where natural openings are few, created openings become important as foraging sites (Wallmo et al. 1972, Regelin et al. 1974, Hershey and Leege 1976). However, as regeneration begins to dominate site productivity, understory vegetation declines (Basile 1975). Maximum understory production in lodgepole pine forests occurred only 10–11 years following either timber harvest (Basile and Jensen 1971) or fire (Lyon 1976) disturbance. Consequently, thinning treatments would lengthen the effective forage-producing interval in forest succession.

TABLE 2. Major plant species within treatment areas, initial production (kg/ha), production after four grazing seasons, and deer and elk diet preferences.

	Control		Moderate		Heavy		Clearcut		Preference[1]	
Species	1976	1980	1976	1980	1976	1980	1976	1980	Deer	Elk
Forbs										
Antennaria spp.	8.1	6.1	4.1	7.0	7.0	3.7	7.2	18.5	+	--
Arnica cordifolia	0.1	5.2	0.3	2.8	1.1	15.2	0.6	5.9	+ +	–
Aster chilensis	0.7	1.5	2.7	4.2	4.8	3.6	8.4	16.3	+	+ +
Astragalus decumbens	38.4	39.7	19.9	33.5	20.1	28.2	26.5	37.9	0	--
Stellaria jamesiana	6.3	9.1	7.9	12.4	6.7	9.9	6.5	8.8	+	+
Taraxacum officinale	18.1	6.5	18.1	14.9	34.6	25.2	15.8	38.1	+	+
12 others	17.7	29.1	13.9	27.0	6.1	17.0	8.9	18.1	+	+
Total	89.4	97.2	66.9	101.8	80.4	102.8	73.9	143.6		
Grasses and Sedges										
Carex brevipes	47.4	23.2	60.5	19.2	62.6	41.8	56.8	42.0	--	--
Carex geyeri	1.1	2.8	11.7	21.3	3.7	7.7	2.1	4.4	--	+
Poa spp.	23.8	12.2	7.6	17.0	14.6	24.9	10.2	40.7	--	--
Sitanion hystrix	0.0	0.0	1.9	0.0	0.0	0.2	3.3	47.7	--	--
5 others	0.0	0.9	0.0	1.1	0.0	5.8	0.0	13.9	--	--
Total	72.3	39.1	81.7	58.6	80.9	80.4	72.4	148.7		
Browse										
Populus tremuloides	14.4	6.0	18.4	6.4	6.9	11.9	0.0	0.9	+	+ +
Rosa nutkana	3.8	4.9	4.7	8.4	25.5	14.2	21.9	23.9	+	+
Salix spp.	0.0	0.0	0.0	0.0	1.1	0.3	2.9	1.6	+	+
4 others	0.0	0.0	0.0	0.6	0.3	0.2	10.2	10.5	+	+
Total	18.2	10.9	23.1	15.4	33.8	26.6	35.0	36.9		
TOTAL	179.9	147.2	171.7	175.8	195.1	209.8	181.3	329.2		

[1] Ratio of % Diet–% production: 0 = no preference (.75–1.50), + = preferred (1.51–4.00), + + = highly preferred (>4.00), – = rejected (.50–.74), -- = highly rejected (<.50).

Our findings indicated an inverse relationship between stand density following thinning and understory vegetal production. Although complete tree removal is untenable on tracts of high site quality, in areas of low timber potential, particularly in stagnated stands, permanent, small openings, consistent with scenic, wildlife, and watershed values (Wyoming Forest Study Team 1971), may be justifiably incorporated into the management plan. Furthermore, both heavy and moderate thinning of regenerating lodgepole pine stands must be considered practical treatments for maintaining or slightly increasing the amount as well as the longevity of the forage resource, particularly when contrasted to the control, which showed a decline in forage production.

Literature Cited

Basile, J. V. 1975. Forage productivity in the lodgepole pine type. Pages 246–263 *in* D. M. Baumgartner, ed., Management of Lodgepole Pine Ecosystems Symposium proceedings. Washington State Univ. Coop. Ext. Serv. 825 pp.

Basile, J. V., and C. E. Jensen. 1971. Grazing potential on lodgepole pine clearcuts in Montana. USDA For. Serv. Res. Pap. INT-98. 11 pp.

Collins, W. B. 1977. Diet composition and activities of elk on different habitat segments in the lodgepole pine type, Uinta Mountains, Utah. Ut. Div. Wildl. Res. Pub. No. 77-18. 74 pp.

Collins, W. B., P. J. Urness, and D. D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. J. Wildl. Manage. 42:799–810.

Deschamp, J. A. 1977. Forage preferences of mule deer in the lodgepole pine ecosystem, Ashley National Forest, Utah. Utah Div. Wildl. Res. Pub. No. 77-16. 75 pp.

Deschamp, J. A., P. J. Urness, and D. D. Austin. 1979. Summer diets of mule deer from lodgepole pine habitats. J. Wildl. Manage. 43:154–161.

Forest Service. 1962. Silvics of forest trees of the United States. Pages 373–387 *in* USDA Agr. Handbook 271. 762 pp.

Hershey, T. J., and T. A. Leege. 1976. Influences of logging on elk on summer range in north central Idaho. Pages 73–80 *in* J. M. Peek and S. R. Hieb, eds., Elk-Logging-Roads Symposium. Univ. of Idaho, Fish, Wildl. and Range Exp. Sta. 134 pp.

Lyon, L. J. 1976. Vegetal development on the Sleeping Child burn in western Montana, 1961 to 1973. USDA For. Serv. Res. Pap. INT-184. 24 pp.

Neff, D. J. 1974. Forage preferences of trained mule deer on the Beaver Creek watersheds. Arizona Game & Fish Dept. Spec. Rep. 4. 61 pp.

Poulton, C. E., and E. W. Tisdale. 1961. A quantitative method for the description and classification of range vegetation. J. Range Manage. 14:13–21.

Regelin, W. L., O. C. Wallmo, J. Nagy, and D. R. Dietz. 1974. Effect of logging on forage values for deer in Colorado. J. For. 72:282–285.

Trappe, J. M. 1959. Lodgepole pine clearcuts in northeastern Oregon. J. For. 57:420–423.

Wallmo, O. C., W. L. Regelin, and D. W. Reichart. 1972. Forage use by mule deer relative to logging in Colorado. J. Wildl. Manage. 36:1025–1033.

Wallmo, O. C., and J. W. Schoen. 1981. Chapter 11, Part 2. Forest Management for deer. Pages 434–448 *in* Mule and black-tailed deer of North America. Wildl. Manage. Institute, Univ. of Nebraska Press, Lincoln. 605 pp.

Wikstrom, J. H., and C. A. Wellner. 1961. The opportunity to thin and prune in the northern Rocky Mountain and intermountain regions. USDA For. Serv. Res. Pap: INT-61. 14 pp.

Wyoming Forest Study Team. 1971. Forest management in Wyoming—timber harvest and the environment on the Teton, Bridger, Shoshone, and Bighorn national forests. USDA For. Serv., Ogden. 41 pp.

HABITAT MANIPULATION FOR REESTABLISHMENT OF UTAH PRAIRIE DOGS IN CAPITOL REEF NATIONAL PARK[1]

Rodney L. Player[2,3] and Philip J. Urness[2]

Abstract.— Utah prairie dogs were transplanted onto the site of a former colony, located in Capitol Reef National Park, Utah. Shrubs on the site were significantly taller than those found on active colonies in similar habitat located on the Awapa Plateau. Therefore, the transplant site afforded a test of the hypothesis that shrub height is a major inhibitory factor affecting occupation of sites by prairie dogs. Four sites of 5 ha each were used. Vegetation treatments—rotobeating, railing, and 2,4-D herbicide—were carried out on three of the sites and the fourth was used as a control. Shrub height and percent cover were significantly reduced on all three treatment sites. Posttreatment effects on the vegetation showed that the greatest percent moisture of the herbage was found on the railed site, followed by the herbicide, rotobeaten, and control sites. Measurements of the visual obstructions to prairie dogs showed that the rotobeaten site had the greatest visibility, followed by the railed, herbicide, and control sites.

Prior to release of prairie dogs on the study area, 200 artificial burrows per treatment were dug, using a power auger. In early summer, 1979, 200 Utah prairie dogs were live-trapped near Loa, Utah. An equal number by sex and age class were released on each treatment. In 1979 a significantly higher number of animals reestablished on the rotobeaten site. In 1980 and 1981 the rotobeaten and railed sites had significantly higher prairie dog numbers than the other sites. Reproduction occurred on both the rotobeaten and railed sites in 1980 and 1981. Results indicated that, when transplanting animals onto sites of former colonies presently overgrown with shrubs, the chances of a successful transplant could be increased by first reducing shrub height and density.

The Utah prairie dog (*Cynomys parvidens*), endemic only to Utah, is presently found in six counties in the south central part of the state (Elmore and Workman 1976). Since 1920 the area occupied by the Utah prairie dog has declined by an estimated 87 percent and their numbers have also declined from an estimated 95,000 in 1920 to an actual count of 3,429 in 1976 (Collier and Spillett 1973). As a result of this decline, the Utah prairie dog was classified as an endangered species in 1968, delisted in 1972, and subsequently reinstated in 1973 (Bureau of Sport Fisheries and Wildlife 1968, 1972, 1973).

Possible reasons for the decline in population and the reduction in range of the Utah prairie dog, as listed by Collier and Spillett (1972), are: purposeful poisoning, disease, drought, shooting, predation, and habitat changes. Poisoning is thought to be the most important factor that has influenced the distribution and abundance of the Utah prairie dog in the past 45 years. Toxicants have been used to eliminate the species from approximately 8000 hectares (Collier and Spillett 1972). Population reductions corresponding to periods of intensive poisoning have occurred in 1933, 1950, and 1960. However, federal agencies have not used toxicants to control Utah prairie dogs since 1963 (Collier and Spillett 1973). Because of its classification as an endangered species, the use of toxicants for population control has been prohibited since 1968.

Prairie dogs of all species are restricted to habitat of relatively open plant communities with short-stature vegetation (Allan and Osborn 1949, Koford 1958, Fitzgerald and Lechleitner 1974, Collier 1974, Crocker-Bedford and Spillet 1977). According to Collier (1974), Utah prairie dogs prefer areas with vegetal cover shorter than 31 cm. Apparently this is due to the fact that prairie dogs are dependent upon visual surveillance of their environment to guard against predators and for intraspecific interactions (Fitzgerald and Lechleitner 1974). Prairie dogs have extended their range into areas where

---

[1] This project was funded by the National Park Service, Cooperative Research Unit, College of Natural Resources, Utah State University. The authors thank the Utah Division of Wildlife Resources, Nongame Wildlife Program, for their cooperation.

[2] Range Science Department, Utah State University, Logan, Utah 84322.

[3] Present address: Forest Service, USDA, Ashley National Forest, Duchesne, Utah 84021.

the tall, dense, native vegetation has been reduced by domestic animals and agriculture (Schaffner 1929, Osborn 1942). The converse of this has also been known to occur. A colony of prairie dogs was eliminated when tall, dense vegetation encroached a site after grazing was stopped (Allan and Osborn 1949).

The recent elimination of the Utah prairie dog in the Escalante Desert was at least in part attributed to an invasion of woody species (Collier and Spillett 1973). Snell and Hlavachick (1980) reported that a colony of black-tailed prairie dogs (*C. ludovicianus*) was reduced in size from 110 acres to 12 acres by allowing cattle to heavily graze the pasture containing the colony in the early spring (thus competing with the prairie dogs for forage) and resting the pasture during June, July, and August, allowing the warm season plants to grow rapidly, creating a visual barrier to the prairie dogs.

A general decrease in grasses and an increase in brushy species has been observed in the Great Basin since settlement in the mid-1800s (Pickford 1932, Cottam and Evans 1945, Blaisdell 1953, Ellison 1960, Tueller and Blackburn 1974). Furthermore, the major foods of prairie dogs (herbaceous species) tend to decline in association with highly competitive, xerophytic shrubs such as big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), and various other shrubs (Ellison 1960, Collier and Spillett 1973, Tueller and Blackburn 1974). This is a result of grazing practices and fire suppression (Pickford 1932, Smith 1949). It should be noted that vegetational changes could have occurred on sites of both occupied and unoccupied colonies. Therefore, although the vegetation on colonies that were eliminated by poisons, disease, predation, shooting, or drought was conducive to prairie dog existence at the time of extirpation, it is possible that subsequent vegetational changes have taken place such that the site is no longer suitable for reestablishment of the colony.

Of the six factors affecting populations of Utah prairie dogs, two (poisoning and shooting) are prohibited because of the endangered classification of this species; man has little or no influence upon three (predation, drought, and disease); and only one of the factors (habitat change) is readily amenable to managerial control.

Efforts to transplant Utah prairie dogs onto sites of former colonies have had limited success. Elmore and Workman (1976:21) stated: "In nearly all historic dogtowns, with few exceptions, sagebrush height and density is the restricting factor for any further reintroduction of the animals." This paper presents the results of a study designed to determine if the success of transplanting Utah prairie dogs onto the site of a historic dogtown could be increased by manipulating the vegetation prior to the reintroduction of the animals.

Study Area and Methods

The study was conducted from 1978–1981 at the site of a former colony of Utah prairie dogs located on Jones Bench in the extreme northwest corner of Capitol Reef National Park in south central Utah. Jones Bench lies within a 25–31 cm precipitation belt, and the elevation is 2200 m. Vegetation on the site was dominated by big sagebrush. Blue grama (*Bouteloua gracilis*) was second most important in terms of canopy cover. Other plant species found in abundance on Jones Bench were: goosefoot (*Chenopodium leptophyllum*), tumbling orach (*Atriplex rosea*), scarlet globemallow (*Sphaeralcea coccinea*), bottlebrush squirreltail (*Sitanion hystrix*), fourwing saltbush (*Atriplex canescens*), and Yellow brush (*Chrysothamnus viscidiflorus*).

Five 5-ha plots were established on Jones Bench. Each plot represented a transplant site. Vegetation measurements were taken on the five sites prior to treatment in 1978, and after treatment in 1979 and 1980. The same measurements were taken on 10 active colonies of Utah prairie dogs located on the Awapa Plateau, approximately 35 km southwest of Jones Bench in 1978. These measurements were taken to determine differences in vegetal characteristics between occupied and unoccupied colonies. The method of vegetational analysis used was that described by Poulton and Tisdale (1961), modified only to the extent of using metric rather than U.S. standard measurements.

Four manipulative treatments were planned. They were rotobeating, railing, herbicide (2,4-D), and fire. The rotobeating was

Table 1. Percent cover and height of plant life forms for an active Utah prairie dog colony on the Awapa Plateau in 1978, and the Jones Bench transplant sites in 1978 (pretreatment), and 1979 and 1980 (posttreatment).

		Shrub		Forb		Grass		Percent bare ground	Percent litter	Percent rock
		Percent cover	Height**	Percent cover	Height	Percent cover	Height			
1978	Awapa Plateau	14.9	24.7	2.9	13.0	3.1	9.4	56.1	14.2	8.8
1978	Rotobeaten	19.2a*	48.3a	0.5	5.8	6.6	7.3	50.6	14.3	8.7
	Railed	18.8a	57.5a	4.1	18.2	1.1	10.5	57.5	16.0	2.5
	Herbicide	17.7a	46.1a	6.6	10.4	2.9	14.7	57.6	11.3	3.9
	Control	25.3a	49.1a	1.3	8.7	1.9	7.3	53.8	13.1	4.6
1979	Rotobeaten	1.8a	14.3a	0.5	8.7	12.5	12.0	40.0	37.3	8.0
	Railed	2.2a	20.4a	0.2	4.6	1.0	13.3	71.3	22.0	3.4
	Herbicide	4.2a	40.8ab	0.1	6.5	4.0	14.6	60.0	27.9	3.7
	Control	21.5b	45.7b	0.5	29.0	2.2	15.4	61.8	10.5	3.6
1980	Rotobeaten	6.9a	30.9a	0.1	10.3	4.3	25.4	22.6	50.3	15.7
	Railed	13.5ab	41.0a	0.3	20.8	0.7	23.1	43.7	33.6	8.2
	Herbicide	6.6a	35.8a	0.1	50.3	1.4	38.2	35.6	47.8	8.4
	Control	22.9b	59.4a	0.0	13.0	0.4	16.5	26.8	38.3	11.5

*For shrubs only, within the same year and column, means followed by the same letters do not differ significantly at the 0.05 level.

**Mean maximum height in centimeters.

accomplished by setting the blades at 10 cm above ground level in order to reduce all vegetation to that height. Railing was accomplished by bolting four medium gauge railroad rails together. This resulted in a 3.75 m long set weighing 71.4 kg per m, which is comparable to one heavy gauge rail. The site was dragged twice in opposing directions. Both the railing and rotobeating treatments were carried out in late August 1978. Attempts to achieve the fire treatment failed because there was insufficient ground cover to carry fire between shrubs. As a result, the fire treatment was dropped from the research plan. The herbicide (2,4-D) was applied by a ground sprayer at the rate of 2.22 kg active ingredient per ha with water (123 1/ha) as a carrier.

Production of herbaceous species was estimated on all transplant sites in August 1979, July 1980, and August 1981. A double-sampling scheme, utilizing a 0.89 m^2 circular plot randomly placed 60 times on each site, was used. Green weight of herbage was ocularly estimated by 3 observers with the average of the three recorded per plant. Of the 60 plots, every fourth one was clipped and the actual weights obtained for estimate correction via regression analysis. These samples were then air dried to determine percent moisture.

Measurements of the visual obstructions to prairie dogs were taken on each transplant site in 1979, 1980, and 1981, and on the site of an active colony on the Awapa Plateau in 1979. A modified version of the technique described by Jones (1968) was used. The method consists of a cover board measuring 65 × 65 cm, with 50 black and 50 white squares each 6.5 × 6.5 cm, arranged in a checkerboard fashion. Thirty readings were taken on each site by randomly placing the board at each site location in one of eight randomly chosen, compass directions. Observations were taken from a height of 30 cm, 20 m from the board. Each site had a maximal count of 3000 squares visible to the investigator. The ratio of actual number of squares counted to the total possible gave a relative percent visibility for each site.

Other characteristics were measured to assure homogeneity of the transplant sites. Measurements of soil depth to an impeding layer up to 1 m were taken on each treatment site. In addition to this, soil texture and color were determined from a soil sample taken from the surface horizon of each site. The degree of slope was estimated to the nearest five degrees for each site using a hand-held clinometer. The aspect to the nearest 1/8 compass interval was also recorded for each site. Differences in these characteristics were relatively small.

Prior to the actual transplanting, approximately 200 artificial burrows, arranged in a matrix, were dug on all sites with a power

TABLE 2. Visual obstruction measurements (30 observations per location) taken on the transplant sites on Jones Bench in 1979, 1980, 1981, and the site of an active colony of Utah prairie dogs on the Awapa Plateau in 1979.

		Location				
		Control	Herbicide	Railing	Awapa Plateau	Rotobeating
Mean	1979	2.9a[*]	7.3a	17.9a	45.5b	50.8b
percent	1980	7.1a	14.3a	11.3a	–	40.6b
visibility	1981	7.8a	10.7a	17.3a	–	44.9b
Number of	1979	21	16	10	4	0
zero	1980	16	11	7	–	1
readings	1981	18	13	11	–	0
Range in	1979	0–31	0–44	0–62	0–83	17–90
percent	1980	0–41	0–52	0–62	–	0–68
visibility	1981	0–34	0–36	0–58	–	14–82

[*] For percent visibility within the same year, means followed by the same letters do not differ significantly at the 0.05 level.

auger. The holes were dug at an angle and were approximately 9 cm in diameter and 60 to 90 cm deep. Torres (1973) reported that only when artificial burrows were dug at angles of 10 to 40 degrees was he successful in reestablishing populations of black-tailed prairie dogs in Colorado. Burrows were dug to provide the animals with temporary protection from predators and adequate thermoregulation.[4]

A total of 200 prairie dogs (50 per site) was transplanted between 16 June and 4 July 1979. The animals were trapped from five colonies located near Loa, Utah. The capture site was the same elevation as the release site. Twenty immature females, 13 immature males, 6 mature males, and 11 mature females were released on each transplant site.

One mature male, one mature female, and two immature animals were placed in three separate cages on each site. This was done to determine if temporarily holding them on the site would more likely assure their permanent location there in contrast to just releasing them on each treatment site (Salmon and Marsh 1981). The cages were constructed of 1 × 2 inch hardware cloth and measured 46 cm high, 77 cm wide, and 122 cm long. Centrally located in the screened bottom of each cage was a 30 × 30 cm hole that was placed over an artificial burrow. Caged animals had free access to water and were fed whole oats and fresh alfalfa daily. All other animals were individually released into artificial burrows located on high relief areas of their respective transplant sites.

All sites were monitored daily in 1979 for animal activity during 23 consecutive days following the release of the first animals. Monitoring took place from elevated locations around the perimeter of the transplant sites. The observer approached close enough to alert the animals (which caused them to stand erect, thus making them more visible), but not so close that they became alarmed and went below ground. Monitoring consisted of taking counts during a 10-minute time period on each transplant site during the morning.

Biweekly monitoring began after 23 days of daily monitoring. This involved taking the same counts but on two consecutive days every other week throughout the summer and early fall of 1979. In 1980 counts were taken 12–13 June and 21–22 July, and in 1981 counts were taken on 1 July (p.m.), 2 July (a.m.), and 5 August (a.m. and p.m.). The highest count obtained for each transplant site during each observation period was used in a randomized block design for evaluating the relative success of the individual transplant sites. The blocks were timed so the variance due to time was eliminated from the evaluation. Through this method it was possible to determine if significant differences occurred between the transplant sites. When significant differences did occur, multiple

---

[4] David F. Balph, Professor, Department of Wildlife Science, Utah State University, personal interview, 14 March 1978.

TABLE 3. Grass and forb production, and percent moisture at the transplant sites on Jones Bench for 1979, 1980, and 1981.

Transplant site	Percent moisture			Herbage production[**]		
	1979	1980	1981	1979	1980	1981
Railed	50a[*]	50a	25ab	151c	295b	203b
Herbicide	46a	55a	49bc	58a	669c	574b
Rotobeaten	45a	37a	30ab	157d	432b	317b
Control	31a	22a	26a	69b	68a	29a

[*] Within a column, means followed by the same letter do not differ significantly at the 0.05 level for herbage production and 0.10 for percent moisture.

[**] Dry weight in kg/ha.

comparisons were made using the LSD test of Fisher (Ott 1977).

RESULTS

Percent cover and height of plant life forms were considered more important than any particular botanical composition because prairie dogs are opportunists that eat any available forage that has nutritional value (Koford 1958, Crocker-Bedford 1976). Therefore, the plant species were grouped according to their life form. Pretreatment shrub height on Jones Bench is the only vegetal measurement taken that showed a significant difference (at the 0.01 level) from that of the shrub height of active colonies. This strengthened the assumption that the pretreatment vegetational height on Jones Bench was too tall for successful transplanting of prairie dogs.

The different treatments had highly varied effects upon the vegetation (Table 1). Percent cover of shrubs, primarily big sagebrush, was the only characteristic that was greatly reduced by all treatments. Shrub cover on manipulated sites differed significantly from the control, with the exception of the railed area the second year after treatment (1980). Shrub height was reduced by railing and rotobeating the first year following treatment (1979), but was not significantly reduced on the herbicide treatment because skeletons of dead plants remained intact. There were no significant differences in shrub height in the second year posttreatment because of rapid recovery of shrubs on the rotobeaten and railed sites. Shrub height on the herbicide area continued to decline slowly as dead plants disintegrated.

Table 2 shows the visual obstruction measurements. With all comparisons (in all years) only those taken on the rotobeaten site do not differ significantly when compared to measurements taken on the site of an active prairie dog colony on the Awapa Plateau.

Although the percent moisture of the herbage varied greatly between transplant sites because of wide variability among the measurements taken within each site (Table 3), significant differences (at the 0.10 level) were found only in 1981. There were significant differences, however (at the 0.05 level), in the total herbage production between the transplant sites. In 1979 all sites differed significantly from one another. In 1980 only the railing and rotobeating sites did not differ significantly, and in 1981 all sites differed significantly from the control.

Table 4 lists results of the animal counts taken during 1979, 1980, and 1981. In 1979 the rotobeating site had significantly higher numbers of animals than the other sites; there were no significant differences between the railed and other sites[5] or between the herbicide and control sites. In 1980 and 1981 no animals were observed on either the control or herbicide sites. In 1980 and 1981 the rotobeaten and railed sites did not differ significantly, but they did differ significantly from all other sites. To a certain extent, prairie dogs were more easily seen on the more open treatments, and this may have affected the counts somewhat. However, the less visible sites were carefully checked for signs of fresh diggings; when such signs were found, these areas were more closely observed.

DISCUSSION

Of the animals placed in cages in an attempt to get them to locate at the release site, all the adults had dug out of their cages within five days; one adult male dug out in

---

[5] Some animals moved to locations near but off the designated transplant sites.

Table 4. Mean numbers of animals counted on Jones Bench during 1979, 1980, and 1981.

	Count sites				
Year	Rotobeaten	Railed	Other[1]	Herbicide	Control
1979 (n = 9)[3]	16.0c	8.1b[2]	3.3ab	1.7a	0.3a
1980 (n = 2)	13.5b(5)[4]	8.5b(3.5)	1.0a	0.0a	0.0a
1981 (n = 2)	15.0b(9)	15.5b(12)	2.0a(1)	0.0a	0.0a

[1] Some animals moved to sites on Jones Bench other than designated transplant sites.

[2] Within the same year, means followed by the same letter do not differ significantly at the 0.05 level.

[3] Number of counts taken during the year.

[4] Mean number of young counted are in parentheses.

less than three hours. On the rotobeaten and railed sites these or other animals occupied some of the cages and their underlying tunnels throughout the first summer. Immature animals were much slower in digging out; some did not dig at all for nine days, so they were released. It is doubtful that immature prairie dogs could survive if they were released in areas without burrows or adult animals to dig burrows.

The longevity of vegetational treatments is related to the amount of brush removed by the treatment (Nielsen and Hinckley 1975). The rotobeaten and railed sites will require retreatment every five to ten years. The herbicide treatment would likely not require such a short retreatment period. In 1981 there was evidence that animals may be moving onto the herbicide site. This is likely because, while other treatments are returning to their pretreatment state, the herbicide is becoming more favorable as habitat. The skeletal remains of the herbicide-killed shrubs are deteriorating; thus visibility for prairie dogs is increasing.

It may be possible to greatly reduce the need for retreatment by combining vegetation treatments. If rotobeating were to be followed in the next year or two by spraying with 2,4-D, then a higher percent kill of shrubs could be attained, as well as an effective reduction of visual obstructions. Treatment could, of course, follow the reverse sequence for the same effect.

The controlled use of fire may be the best technique to achieve the desired results where fuel loading is sufficient to allow burning. Fire, if carried out properly, could remove a high percentage of nonsprouting shrubs and increase visibility immediately at low cost. With such results it is likely that retreatment would not be necessary for perhaps 20 years or more. Fire would also release many grasses and forbs for increased growth, thus making the site even more favorable for prairie dog reestablishment through increased food resources.

The negative response of transplanted animals to the control site was a strong indication that some type of vegetal treatment is necessary when transplanting animals onto sites of former colonies presently overgrown with shrubs. The chances of a successful transplant could be increased by first reducing shrub height and cover. Our study should aid in reestablishing scattered colonies of Utah prairie dogs throughout their former range to help assure the continued existence of this unique animal. One objective of this effort is to restore sufficient healthy populations on public lands to allow for delisting of this animal as an endangered species and thus reduce conflicts on private lands by permitting local control on agricultural problem areas.

Literature Cited

Allan, P. F., and B. Osborn. 1949. Vegetation of an abandoned prairiedog town in tall grass prairie. Ecology 30:322–332.

Blaisdell, J. P. 1953. Ecological effects of planned burning of sagebrush: grass range on the upper Snake River Plains. USDA Tech. Bull. 1075. 39 pp.

Bureau of Sport Fisheries and Wildlife. 1968. Rare and endangered fish and wildlife of the United States. U.S. Govt. Print. Off., Washington, D.C. 153 pp.

_____. 1972. Rare and endangered fish and wildlife of the United States. U.S. Govt. Print. Off., Washington, D.C. 272 pp.

_____. 1973. Rare and endangered fish and wildlife of the United States. U.S. Govt. Print. Off., Washington, D.C. 289 pp.

Collier, G. D. 1974. The Utah prairie dog: abundance, distribution, and habitat requirements. Unpublished dissertation. Utah State Univ., Logan. 96 pp.

COLLIER, G. D., AND J. J. SPILLETT. 1972. Status of the Utah prairie dog (*Cynomys parvidens*). Utah Acad. Sci., Arts, and Lett. 49:27–39.

______. 1973. The Utah prairie dog—decline of a legend. Utah Science 34:83–87.

CROCKER-BEDFORD, D. C. 1976. Food interactions between Utah prairie dogs and cattle. Unpublished thesis, Utah State Univ., Logan. 118 pp.

CROCKER-BEDFORD, D. C., AND J. J. SPILLETT. 1977. Home ranges of Utah prairie dogs. J. Mammal. 58:63.

COTTAM, W. P., AND F. EVANS. 1945. A comparative study of the vegetation of grazed and ungrazed canyons of the Wasatch Range, Utah. Ecology 26:171–181.

ELLISON, L. 1960. Influences of grazing on plant succession of rangelands. Bot. Rev. 26:1–78.

ELMORE, S., AND G. WORKMAN. 1976. A baseline study of the past and present status of the Utah prairie dog (*Cynomys parvidens*) in Bryce Canyon National Park. Utah State Univ., Dept. Wildl. Sci., Logan. 40 pp.

FITZGERALD, J. P., AND R. R. LECHLEITNER. 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. Am. Midl. Nat. 92:142–163.

JONES, R. E. 1968. A board used to measure cover used by prairie grouse. J. Wildl. Manage. 32:28–31.

KOFORD, C. B. 1958. Prairie dogs, white faces and blue grama. Wildl. Monog. 3:1–78.

NIELSEN, D. B., AND S. D. HINCKLEY. 1975. Economic and environmental impacts of sagebrush control on Utah's rangelands. A review and analysis. Utah Agric. Expt. Sta. Res. Rept. No. 25. 27 pp.

OSBORN, B. 1942. Prairie dogs in shinnery (oak scrub) savannah. Ecology 23:322–332.

OTT, L. 1977. An introduction to statistical methods and data analysis. Duxbury Press, North Scituate, Massachusetts. 730 pp.

PICKFORD, G. D. 1932. The influences of continued heavy grazing and promiscuous burning on spring-fall ranges in Utah. Ecology 13:159–171.

POULTON, C. E., AND E. W. TISDALE. 1961. A quantitative method for the description and classification of range vegetation. J. Range Manage. 14:13–21.

SALMON, T. P., AND R. E. MARSH. 1981. Artificial establishment of a ground squirrel colony. J. Wildl. Manage. 45(4):1016–1018.

SCHAFFNER, J. H. 1929. Extension of the natural range of two mammals in Clay County, Kansas. Trans. Kansas Acad. Sci. 31:61–62.

SMITH, A. D. 1949. Effects of mule deer and livestock upon foothill range in northern Utah. J. Wildl. Manage. 13:421–423.

SNELL, G. P., AND B. D. HLAVACHICK. 1980. Control of prairie dogs—the easy way. Rangelands 2(6):239–240.

TORRES, J. R. 1973. Status of the black-tailed prairie dog and the black-footed ferret in North Dakota. Pages 51–59 *in* Proceedings of the Black-Footed Ferret and Prairie Dog Workshop. South Dakota State Univ., Brookings. 208 pp.

TUELLER, P. T., AND W. H. BLACKBURN. 1974. Condition and trend of the big sagebrush/needle-and-thread grass habitat type in Nevada. J. Range Manage. 27:36–40.

EFFECTS OF DEFOLIATION ON REPRODUCTION OF A TOXIC RANGE PLANT, *ZIGADENUS PANICULATUS*

V. J. Tepedino[1]

Abstract.— The effect of complete defoliation, prior to flower stalk appearance, on the reproductive success of foothill deathcamas, a toxic range plant, was studied in northern Utah. Defoliated plants did not replace their leaves. Defoliation had no effect on total number of flower stalks produced but did significantly slow the rate of stalk emergence and reduce the number of plants that produced open flowers. The number of leaves produced by control plants was also positively associated with the probability of producing a flowering stalk. Few plants in either defoliated or control treatments set seed, probably because of inactivity of pollinators during a cold and wet spring. It is suggested that species, such as deathcamas, which either produce leaves early in spring or are liliaceous geophytes, may be especially vulnerable to herbivory.

Among the characteristics thought to render plant species "apparent," or relatively easy for herbivores to find, are the perennial habit and large size, both of individuals and of populations (Feeney 1976, Rhoades and Cates 1976, Rhoades 1979). Apparent species are also hypothesized to reduce their susceptibility to herbivory by diverting relatively large amounts of energy from vegetative and reproductive functions to the production of antiherbivore compounds.

Foothill deathcamas (*Zigadenus paniculatus* [Nutt] S. Wats; Liliaceae) is a bulb-forming range plant of the western U.S. (James et al. 1980) that possesses some of these characteristics of apparency: it is perennial and is commonly found in large numbers throughout its range, although individual plants are small. Apparency is further increased because deathcamas is among the first species to produce leaves in the spring (James et al. 1980, pers. obs.): it is therefore extremely attractive to mammalian herbivores that have subsisted on low-quality forage through the winter. Despite their availability, few plants ($\approx$ 10.0 percent) display any evidence of herbivory (Tepedino, unpubl. ms.), evidently because of the numerous steroid alkaloids present in the leaves and other plant parts (Willaman and Li 1970) that are toxic to mammals (Marsh and Clawson 1922).

In addition to the apparently large commitment to the defense of leaf tissue by the production of alkaloids, there are other reasons for suspecting deathcamas to be particularly vulnerable to herbivory when it occurs. Although most perennials typically replace their leaves soon after defoliation (Jameson 1963, Kulman 1971, Rockwood 1974), evidence suggests that geophytic species of the Liliales may be incapable of doing so (Heath and Holdsworth 1948); under normal conditions, once the presumptive flower stalk bud is formed in early spring no further leaf initials are cut. Also, a minimum number of leaves has been shown to be necessary for flower stalk production for several liliaceous species (Heath and Holdsworth 1948 and references therein). Thus, defoliation of deathcamas may significantly impair reproductive success by lowering the number of flowers or seeds produced. The relationship between the number of leaves and flowers produced and the effect of artificial defoliation on reproductive success are reported here.

Methods

The study site (alt. 1400m) was at the top of a west-facing embankment, 8 km south of Avon, Utah (Cache Co.), along County Road 165. Here numerous deathcamas plants grew among sagebrush (*Artemisia* sp.) and associated forbs.

---

[1] USDA-ARS-WR, Bee Biology and Systematics Laboratory, Utah State University, UMC 53, Logan, Utah 84322.

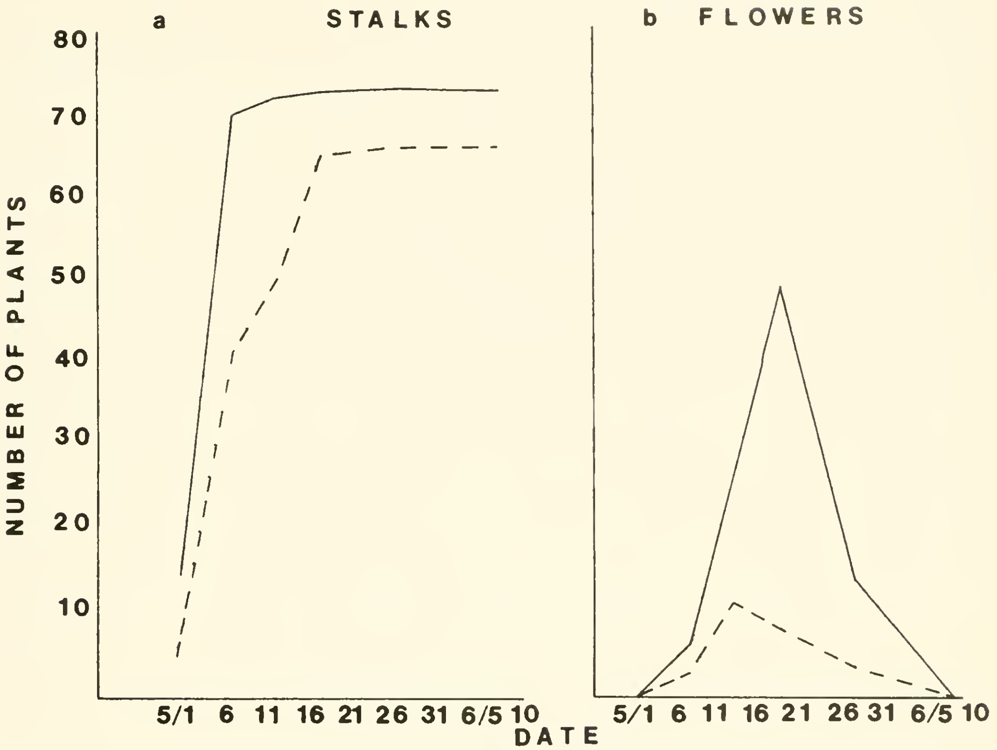


Fig. 1. Number of plants producing a, flowering stalks; b, open flowers for defoliation (dashed line); and control (solid line) treatments.

Foothill deathcamas produces 3–9 basal leaves from a tunicate bulb in early spring, followed by a single paniculate flowering stalk 4–6 weeks later. Plants with 5 or more leaves were completely defoliated on 23 April 1981 after the basal leaves were fully extended, but before appearance of the flowering stalk. Leaves of 100 plants were counted and removed at soil level with a razor blade. At the same time, a plant nearby (between 1–2 m) each of those treated was selected as a control. Leaves of controls were also counted. All plants were marked with plastic labels.

Plants were subsequently examined at approximately weekly intervals for developmental stage of the flowering stalk. Absence or presence of the stalk, presence of open or spent flowers, and fruit maturation (judged by expansion of the perianth) were recorded.

Precipitation and temperature records were obtained from a Utah State University weather station located 19 km north of the site at similar elevation.

RESULTS

Unlike some other perennial species, *Z. paniculatus* did not replace lost leaf tissue; once defoliated, experimental plants remained in that condition for the rest of the growing season.

Flowering stalks of plants from both treatments had begun to emerge by the first examination date (1 May). However, the rate of emergence was slower for defoliated plants than for controls (Fig. 1a); a chi-square test of equal distribution of plants with flowering stalks in each treatment was significant for the first three sampling dates (1 May, $X^2 = 3.86$, $P = 0.05$; 7 May, $X^2 = 7.58$, $P<0.01$; 12 May, $X^2 = 3.97$, $P = 0.05$). Although flowering stalks of defoliated plants emerged more slowly, by the end of the flowering season there was no significant difference between treatments in the total number of stalks produced ($X^2 = 0.35$, $P<0.50$).

The major difference between defoliated and control plants was in the number of flowering stalks that produced open flowers

(Fig. 1b). Only 21 of the 66 stalks produced by defoliated plants developed open flowers as compared to 59 of 71 control stalks. (Two additional control stalks were decapitated by herbivores before they flowered). Flower buds on most stalks of defoliated plants withered soon after the stalks emerged, and stalks subsequently turned brown.

Few plants of either treatment set seeds. Only one defoliated plant, and five control plants produced seeds. Lack of seed set by control plants was probably due to inactivity of pollinators caused by cold and rainy weather. Precipitation fell on 15 of 31 days in May and the maximum temperature was below 21 C (70 F) on 18 days. Only 7 days were both rainfree with maximum temperature at or above 21 C, and all these came at the beginning or end of the month (days 1, 2, 25, 28–31).

The number of leaves produced by a plant was associated with stalk production for both treatments. Table 1 shows the distribution of plants by leaf number categories; the overall distribution did not differ significantly between treatments ($X^2 = 1.38$, d.f. $= 3$; in this and the following analysis leaf number categories have been combined when expected values were <5.0, Maxwell [1961]). For each treatment the proportion of plants producing stalks increased with leaf number (Table 1). A comparison of the number of plants in each leaf category that produced stalks with those that did not was significant for both treatments (defoliated, $X^2 = 7.2$, d.f. $= 2$, $P<0.05$; control, $X^2 = 12.2$, d.f. $= 1$, $P<0.001$): plants with more leaves had a greater probability of producing a stalk even when leaves had been removed. A comparison between treatments of the distribution of plants with stalks by leaf number showed no significant difference ($X^2 = 0.06$, d.f. $= 2$, $P<0.50$).

Plants with more leaves also exhibited a greater tendency to produce open flowers (Table 1). However, when plants producing flowers were compared by leaf number with plants producing only stalks, differences between treatments were apparent. For control plants the distributions did not differ significantly ($X^2 = 0.96$, d.f. $= 1$); if a plant sent up a stalk, there was a high probability (80.8 percent) that flowers would open, irrespective of leaf number. For defoliated plants there was a greater probability for plants that had produced more leaves to produce some open flowers on the stalk than for those with fewer leaves ($X^2 = 3.36$, d.f. $= 1$, $P = 0.07$).

DISCUSSION

Defoliation had irreparable effects on the reproductive potential of *Z. paniculatus.* Although removal of leaves just before stalk emergence did not affect the likelihood of producing a stalk, it did significantly delay the emergence of stalks and reduce the probability that any flower buds would reach anthesis. These results are in general agreement with other studies that have shown that simulated herbivory can significantly reduce numbers of flowers (Blaisdell and Pechanec 1949, Callan 1949, Simmonds 1951, Mueggler 1967, Enyi 1975) or seeds (Sackston 1959, Rockwood 1974, Enyi 1975), and also delay flowering (Collins and Aitken 1970) (see Jameson 1963, Kulman 1971 for reviews).

The effects of defoliating deathcamas, however, may be more profound than the simple elimination of a single year's reproduction. The results suggest that stored carbohydrates from the previous year are depleted in the production of leaves. Leaves, in turn, hasten emergence of the stalk, and are required for maturation of flowers, seeds, and the synthesis of storage material for the subsequent year's vegetative growth. But, unlike many other perennials, *Z. paniculatus* is apparently unable to produce a second crop of leaves after defoliation. If leaves are cropped

TABLE 1. Distribution of defoliated and control plants by number of leaves/plant, and the percentage of total plants in each category that produced flowering stalks and open flowers.

	Number of leaves				
	5	6	7	8	9
Defoliated					
Total no.	0	13	53	29	5
With stalk (%)	0.0	38.5	64.2	75.9	100.0
With flowers (%)	0.0	15.4	13.2	34.5	40.0
Control					
Total no.	2	8	60	24	6
With stalk (%)	0.0	25.0	70.0	95.8	100.0
With flowers (%)	0.0	25.0	53.3	83.3	83.3

before stalk emergence, plants may have had insufficient photosynthetic surface to produce storage material for the following year. Thus, it is possible that a single defoliation episode is sufficient to cause either death of the plant or to eliminate reproduction for more than one year. If this proves to be the case, the production of antiherbivore compounds becomes important.

The positive relationship between the number of leaves produced and the likelihood of sending up a flowering stalk has also been reported for other species in the Liliales (Heath and Holdsworth 1948). These results suggest that the number of leaves produced increases with age of the plant, and that plants do not begin flowering until the second or third year. This assertion needs more careful examination; however, numerous plants with 3–5 leaves in a population at higher altitude (1850 m) have been observed both to bloom and produce seeds (Tepedino, unpubl. ms.).

Schemske et al. (1978) showed that seed production in self-incompatible spring-flowering herbs can vary considerably from year-to-year, and suggested that this variation was due to the effect of unpredictable spring weather on pollinators. A similar explanation seems appropriate for Z. *paniculatus*, which also requires insects for pollination (Tepedino 1981). Few plants in the control treatment set seed, and this was associated with an absence of pollinators during an extended period of cold and wet weather. Conversely, in the previous year, when weather was more conducive to insect activity, most plants set seed at a nearby site (pers. obs.).

Two characteristics of the growing season and life form of Z. *paniculatus* suggest possible modifications of the concept of plant apparency. First, as noted above, plant species that leaf out early in spring are extremely apparent to mammalian herbivores, and we should expect the leaves of such plants to be well defended. This seasonality component of apparency seems to have been previously ignored. A cursory perusal of James et al. (1980) suggests that 75–80 percent of the plants most poisonous to livestock in the western U.S. begin growth in early spring, so the idea would seem to deserve further attention.

Second, several workers have noted that, among the monocots, only the Liliales are well represented in the number of species that produce alkaloids (Hegnauer 1966, Levin and York 1978). Tomlinson (1980) has pointed out that many of these species are geophytes. Perhaps the leaves of many of these species are irreplaceable, as in deathcamas and other liliaceous species (Heath and Holdsworth 1948), and must therefore be heavily defended against herbivory.

Acknowledgments

I thank K. Ruggeri, T. Peery, and M. Schultz for help with the field work and data tabulation; T. Waldron for inking the figure; and D. R. Frohlich and Drs. E. Bach Allen and I. Palmblad, Utah State University, for commenting on the manuscript.

Literature Cited

Blaisdell, J. P., and J. P. Pechanec. 1949. Effects of herbage removal at various dates on vigor of bluebunch wheatgrass and arrowleaf balsamroot. Ecology 30:298–305.

Callan, E. M. 1949. Effect of defoliation on reproduction of *Cordia macrostachya*. Bull. Entomol. Res. 39:213–15.

Collins, W. J., and Y. Aitken. 1970. The effect of leaf removal on flowering time in subterranean clover. Aust. J. Agric. Res. 21:893–903.

Enyi, B. A. C. 1975. Effects of defoliation on growth and yield in groundnut (*Arachis hypogea*), cowpeas (*Vigna unquiculata*), soybean (*Glycine max*), and green gram (*Vigna aurens*). Ann. Appl. Biol. 79:55–66.

Feeny, P. 1976. Plant apparency and chemical defense. Rec. Adv. Phytochemistry 10:1–40.

Heath, O. V. S., and M. Holdsworth. 1948. Morphogenic factors as exemplified by the onion plant. Sym. Soc. Exp. Biol. 2:326–350.

Hegnauer, R. 1966. Comparative phytochemistry of alkaloids. Pages 211–230 *in* T. Swain, ed., Comparative phytochemistry. Academic Press, New York.

James, L. F., R. F. Keeler, A. E. Johnson, M. C. Williams, E. H. Cronin, and J. D. Olsen. 1980. Plants poisonous to livestock in the western states. USDA Agric. Infor. Bull. 415. 90 pp.

Jameson, D. A. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532–594.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Annu. Rev. Entomol. 16:289–324.

Levin, D. A., and B. M. York, Jr. 1978. The toxicity of plant alkaloids: an ecogeographic perspective. Biochem. Syst. Ecol. 6:61–76.

Marsh, C. D., and A. B. Clawson. 1922. The deathcamas species, *Zygadenus paniculatus* and *Z. elegans*, as poisonous plants. USDA Bull. No. 1012. 25 pp.

Maxwell, A. E. 1961. Analysing qualitative data. Methuen, London.

Mueggler, W. F. 1967. Response of mountain grassland vegetation to clipping in southwestern Montana. Ecology 48:942–949.

Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. Pages 3–54 *in* G. A. Rosenthal and D. H. Janzen, eds., Herbivores: their interaction with secondary plant metabolites, Academic Press, New York.

Rhoades, D. F., and R. G. Cates. 1976. Toward a general theory of plant antiherbivore chemistry. Rec. Adv. Phytochemistry 10:168–213.

Rockwood, L. L. 1974. The effect of defoliation on seed production of six Costa Rican tree species. Ecology 54:1363–1369.

Sackston, W. E. 1959. Effects of defoliation on sunflowers. Can. J. Plant Sci. 39:108–118.

Schemske, D. W., M. F. Willson, M. N. Melampy, L. J. Miller, L. Verner, K. M. Schemske, and L. B. Best. 1978. Flowering ecology of some spring woodland herbs. Ecology 59:351–66.

Simmonds, F. J. 1951. Further effects of the defoliation of *Cordia macrostachya* (Jacq.) R. and S. Canadian Entomol. 83:24–27.

Tepedino, V. J. 1981. Notes on the reproductive biology of *Zigadenus paniculatus*, a toxic range plant. Great Basin Nat. 41:427–430.

Tomlinson, P. B. 1980. Monocotyledonous habit in relation to morphology and anatomy. Sym. Linn. Soc. London 8:7–19.

Willaman, J. J., and H. L. Li. 1970. Alkaloid-bearing plants and their contained alkaloids. Lloydia (supplement) 33 (3A). 286 pp.

DISTRIBUTION AND RELATIVE ABUNDANCE OF FISH IN RUTH RESERVOIR, CALIFORNIA, IN RELATION TO ENVIRONMENTAL VARIABLES[1]

Steven Vigg[2] and Thomas J. Hassler[3]

Abstract.— The fish population of Ruth Reservoir, California, was sampled every two weeks with variable mesh gill nets from May 1974 through May 1975. Fish were captured in the following order of numerical abundance: Humboldt sucker (*Catostomus humboldtianus*), golden shiner (*Notemigonus crysoleucus*), brown bullhead (*Ictalurus nebulosus*), white catfish (*I. catus*), rainbow trout (*Salmo gairdneri*), and largemouth bass (*Micropterus salmoides*). The three most abundant species made up about 95 percent of total numbers and weight. All species exhibited a similar cyclic temporal availability pattern: catch rates increased to a maximum during summer and fall and decreased during winter and spring. Environmental variables with the most pronounced relationships to fish catches were temperature (direct) and turbidity (inverse).

Information on Ruth Reservoir fish ecology collected prior to this study was limited; data consisted of stocking records, yearly creel survey data on opening weekends of the fishing season, five gill net sets during November 1968, and the results of a reward tagging program for salmonids during May 1972 (Ruth Reservoir file, California Department of Fish and Game, Eureka). Management measures have consisted primarily of stocking hatchery-reared salmonids. Unauthorized introductions of exotic species into the reservoir have also been made.

Alterations to the dam have been proposed that would affect the physical and chemical characteristics of the lake and thus the aquatic organisms, specifically the fish populations. The present dam may be modified or replaced by a larger structure to meet future water needs (U.S. Army Corps of Engineers 1973). Air-induced circulation and a multilevel discharge structure have been proposed to reduce downstream turbidity (Winzler and Kelly 1975).

The objectives of this study were to determine the relative abundance and distribution of fish in Ruth Reservoir and determine their relation to environmental variables.

Study Area

Ruth Reservoir is impounded behind R. W. Matthews Dam, near the headwaters of the Mad River in Trinity County, California (Fig. 1). This water supply reservoir, about 127 km by river from the Pacific Ocean, provides municipal and industrial water for the Humboldt Bay Area. The dam was completed in 1961 and is operated by Humboldt Bay Municipal Water District (HBMWD). The reservoir has a maximum surface area of 445.2 ha, a maximum storage capacity of 63.9 million cubic meters, a mean depth of 14.4 m at maximum pool, and a minimum discharge of 142 liters per second.

Annual water level fluctuations have ranged from 9.8 to 15.5 m, with a mean fluctuation of 12.6 m (HBMWD, unpublished data). The water level is usually lowest in November and highest in January. The highest recorded water level, 5.8 m above spillway elevation, was on 22 December 1964, and the lowest, 13.7 m below spillway elevation, on 29 November 1967. Water level fluctuated 14.4 m during the study.

The reservoir is 11.3 km long at full pool and has a mean width of 0.6 km (Winzler and

---

[1] Cooperators include the California Department of Fish and Game and the United States Fish and Wildlife Service.

[2] Bioresources Center, Desert Research Institute, P.O. Box 60220, Reno, Nevada 89506.

[3] California Cooperative Fishery Research Unit, Humboldt State University, Arcata, California 95521.

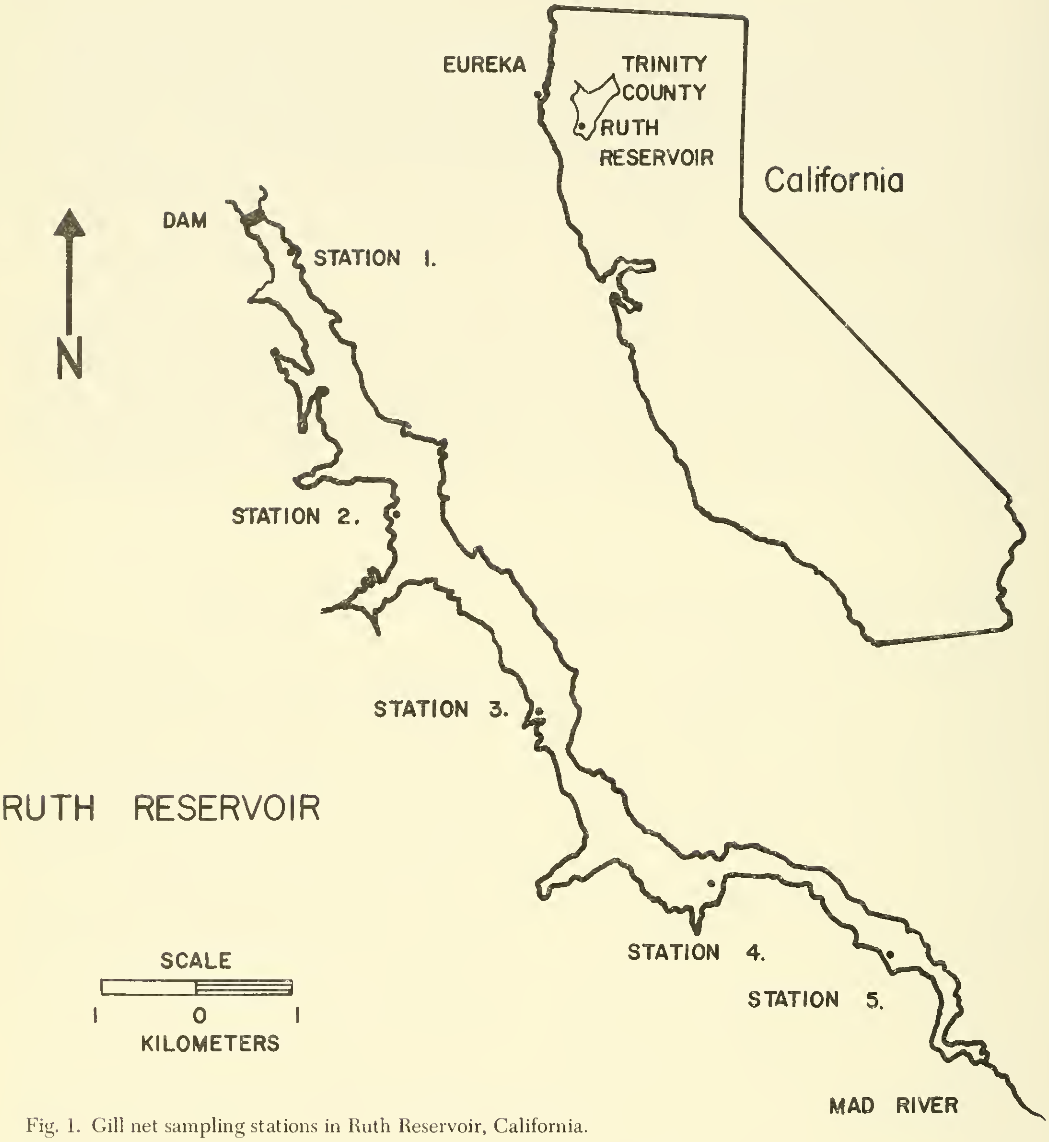

EUREKA
TRINITY COUNTY
RUTH RESERVOIR
California
N
DAM
STATION 1.
STATION 2.
STATION 3.
RUTH RESERVOIR
STATION 4.
STATION 5.
SCALE
1 0 1
KILOMETERS
MAD RIVER

Fig. 1. Gill net sampling stations in Ruth Reservoir, California.

Kelly 1975). Several small tributaries flow into the reservoir, but the major inflow is from the Mad River, which has a watershed of 30,822 ha above the dam (Iwatsubo et al. 1972). The dominant geological feature of the watershed is the Franciscan Formation. Heavy precipitation, steep slopes, and unstable geology have resulted in high erosion in this area (Young 1971). The primary influx of sediment corresponds to major precipitation from November through April. During the rainy season, large amounts of fine suspended sediment are distributed throughout the mixed reservoir; surface turbidity diminishes by late spring as the suspended particles settle and thermal stratification confines suspended sediments to the bottom zone, thus developing a turbid density current (Winzler and Kelly 1975). Persistent turbidity occurs in the reservoir and downstream from the reservoir's bottom discharge.

Surface water temperatures range from 0 to 26.7 C; the minimum generally occurs in December or January, and the maximum in July or August. Bottom temperatures range from less than 4 to as high as 17 C. The reservoir has characteristic spring and fall overturns of a dimictic lake. Dissolved oxygen

(DO) ranges from saturation to seasonal anaerobic bottom deficits (California Department of Water Resources, Red Bluff, 1969).

METHODS

Sampling was conducted at two-week intervals from May 1974 to May 1975; 26 samples—7 each in summer and fall and 6 each in winter and spring—were analyzed by season. The seasons were defined as follows: summer, 1 June to 31 August; fall, 1 September to 1 December; winter, 2 December to 2 March; and spring, 3 March to 31 May. Five gill net sampling stations were established from the dam to reservoir headwaters (Fig. 1).

Fish populations were sampled with bottom set, variable mesh gill nets 1.83 × 54.86 m comprising six 9.14-m panels of the following mesh sizes (bar measure): 1.27, 1.91, 2.54, 3.18, 3.81, and 6.35 cm. All mesh sizes were made of number 104 multifilament white nylon except the 6.35-cm mesh, which was number 139.

The nets were set in the late evening and fished overnight for 12 to 16 hours. Fish catch was adjusted to a standard 12-hour set. The net was anchored in approximately 2 m of water at the inshore end and set perpendicular to shore. The end of the net placed closest to shore was randomized. Each gill net panel was marked with a painted vertical stripe to give two replicates for each set. Fish catch from the right and left halves of each mesh size was recorded separately and randomly assigned to one of two derived replicates. The data could thus be treated as replicate 27.43 m variable mesh nets in each location at each time, enabling the use of a nested analysis of variance design.

Limnological data were obtained during each sampling period at each station. Temperature, turbidity, conductivity, and DO were measured at limnetic stations corresponding to the gill net stations. Water samples were taken with a 2-l water bottle, 1 m below the surface, at middepth, and 1 m above the bottom. Immediately upon bringing the sample to the surface we measured temperature with a mercury bulb thermometer, or the thermistor of the DO meter. A bathythermograph was used to measure depth-temperature profiles. Turbidity, Jackson Turbidity Units (JTU), was measured with a Hach Model 1860 Turbidimeter. A Beckman Solu Bridge was used to measure electroconductivity, recorded as micro mhos per centimeter (μmho/cm) at 25 C. Dissolved oxygen determinations were made with a Hach Model CA-10 DO kit (June through October) and a Delta Scientific Model 85 DO Meter (November through May). Surface and discharge temperature, reservoir surface elevation, inflow, and discharge data were obtained from HBMWD records.

To detect significant differences in horizontal and seasonal fish distribution, and interaction between reservoir area and season, we analyzed the catch-per-unit-of-effort data by using a two-way nested analysis of variance design computer program. Fish relative abundance was analyzed by sampling station and season. One-way analysis of variance (Sokal and Rohlf 1969) was used to analyze seasonal differences in mean fish catch at Station 5. This station was dewatered by seasonal low water and was not included in the overall analysis. Fish catch data were transformed:

$(\log_{10}(Y+1))$ where Y = fish catch.

TABLE 1. Gill net catches at five sampling stations in Ruth Reservoir from May 1974 through May 1975.

Species		Relative abundance			Relative biomass (weight, g)		
Common name	Scientific name	Catch/h	Number	Percent of total	Mean	Total	Percent of total
Humboldt sucker	*Catostomus humboldtianus*	1.06	1,854	42.5	452.0	838,008	76.3
Golden shiner	*Notemigonus crysoleucus*	0.82	1,432	32.8	53.8	77,042	7.0
Brown bullhead	*Ictalurus nebulosus*	0.51	888	20.3	149.9	133,111	12.1
White catfish	*I. catus*	0.08	141	3.2	262.5	37,013	3.4
Rainbow trout	*Salmo gairdneri*	0.02	28	0.6	258.0	7,224	0.7
Largemouth bass	*Micropterus salmoides*	0.01	23	0.5	276.0	6,348	0.6
Total		2.49	4,366	100	–	1,098,746	100

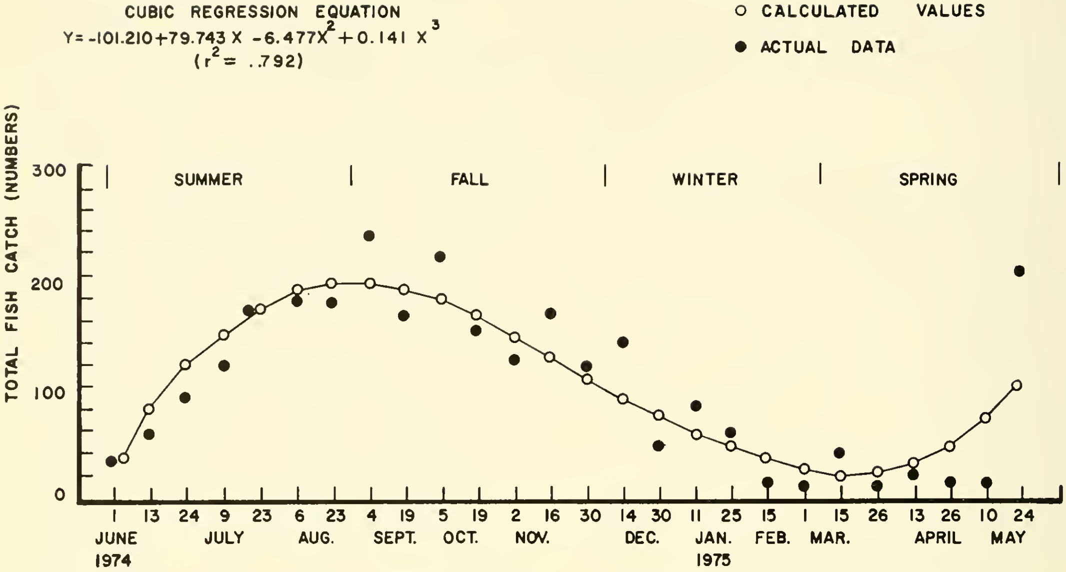


Fig. 2. Relationship between time and total fish catch in Ruth Reservoir, June 1974 through May 1975.

Correlation analysis was used to determine relationships between environmental factors and fish catch (by species and station). Product-moment correlation coefficients (r) between environmental parameters and fish catch were determined and tested for significance. We included variables with meaningful biological relationships that were significantly correlated with fish catch in multiple linear correlation analyses using the method of least squares (Cooley and Lohnes 1971).

Results

Species Composition and Relative Abundance

Humboldt sucker, *Catostomus humboldtianus*, the most abundant of the six fish species in the net catches, accounted for over 42 percent of the numbers of fish and over 76 percent of the weight (Table 1). Numerically, golden shiner, *Notemigonus crysoleucus*, was second in abundance and brown bullhead, *Ictalurus nebulosus*, third. Over 1.5 times as many shiners were captured as bullheads; however, the biomass of brown bullheads was over 1.7 times greater than that of golden shiners. White catfish, *Ictalurus catus*, made up slightly over 3 percent in terms of numbers and weight. Largemouth bass, *Micropterus salmoides*, and rainbow trout, *Salmo gairdneri*, accounted for less than 1 percent of the catch.

Humboldt suckers and rainbow trout were the only fish captured in Ruth Reservoir that were established in the upper Mad River drainage prior to impoundment. The reservoir has been stocked yearly with rainbow trout from various hatcheries. The coho salmon, *Oncorhynchus kisutch*, was introduced in 1972, and the Japanese ayu, *Plecoglossus altivelis*, in 1964–1965. Neither of these two species was taken in the net catches.

Distribution

A total of 4366 fish were caught in 1756 gill net hours. Total catch was highest during late summer and early fall, greatly decreased during winter and early spring, and remained low until late spring (Fig. 2). All species showed a cyclic seasonal trend (Fig. 3). The increased catch of golden shiners in the spring sample was most evident, and accounted for 52 percent of the total spring catch.

Total catch was consistently higher at the upper end of the reservoir (Stations 4 and 5) during all seasons, accounting for 55 to 86 percent of the catch (Table 2). Catches were most evenly distributed during fall, when

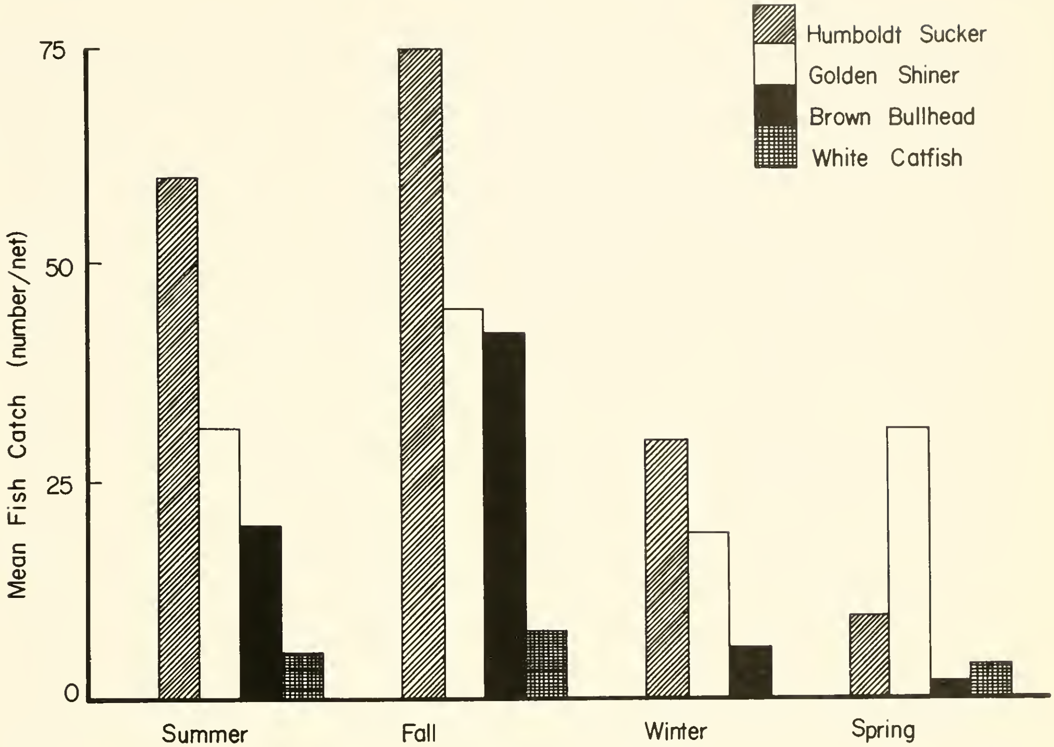


Fig. 3. Mean fish catch by species and season in Ruth Reservoir, 1974–1975.

about 45 percent of the fish were taken at the lower three stations. Catches of Humboldt suckers, golden shiners, and brown bullheads illustrate this trend of higher abundance at upper reservoir stations. Catches of white catfish were more evenly distributed throughout the reservoir; but were slightly higher in the middle and lower than in the upper reservoir areas.

Humboldt suckers were generally more abundant in catches than other species during all seasons. However, during summer and fall catches of brown bullhead were highest. Golden shiner catches were relatively high during summer at Station 5 and during spring at Stations 2 and 4. White catfish were the second or third most abundant species in the catch at the lower end of the reservoir (Stations 1 and 2) during all seasons except winter, when only one was captured in the entire lake.

Temporal and spatial fish distribution patterns were summarized by analysis of variance. Mean catches of Humboldt suckers, golden shiners, brown bullheads, and total species were significantly different ($P<0.01$) with respect to season and station. The mean catch of white catfish differed significantly by season ($P<0.001$) but not by station. A significant interaction for catches of brown bullhead by season and station ($P<0.01$) indicated that seasonal distribution was not consistent on a spatial basis. There was a large difference in seasonal mean catches of bullhead in the upper end of the reservoir, but catches in the lower end were consistently low and not greatly different. There was no significant interaction for Humboldt sucker, golden shiner, white catfish, and total catch. Thus, mean seasonal catch for these species was independent of lake area effects and, conversely, differences in area fish catch were significant, regardless of season.

There was a significant difference in replicates within season and station for all species ($P<0.005$). Seasons were not biologically discrete units of time, i.e., temporal trends of fish catch existed within seasons.

At station 5 total species mean catch was significantly higher for the summer-fall than for winter-spring ($P<0.001$, Table 3). There was a significant difference in mean catch of brown bullhead ($P<0.001$) and golden shiner ($P<0.05$) between the two time periods. Catches of both species were higher during summer and fall than during winter and spring. There was no significant difference in the catches of Humboldt sucker and white catfish between the two time periods. Temporal catch trends within the time periods are indicated by the significant differences in replicates for all species except the white catfish, which was scarce in catches during both periods.

Environmental Variables

Fish catch and limnological data were tabulated by sample period, station, and depth (Vigg 1979). Seasonal variations of environmental parameters were pronounced (Table 4). Temperature was highest during August (maximum 27.0 C), and lowest in late December (1.0 C). The surface DO concentration was never below 8.0 mg/l. Bottom DO deficits occurred during August and September. During early August, when maximum annual water temperatures occurred in the upper end of the reservoir, bottom DO decreased there to 2 mg/l. Bottom DO was depleted in midreservoir in late August and in the lower end in September (Fig. 4). This DO depletion trend probably indicated either movement of the low-oxygen water mass down reservoir or differential in-place bottom DO depletion, or both. Destratification and mixing in the upper end of the reservoir in late August resulted in high DO concentrations (10 mg/l) throughout the water column. Destratification and reoxygenation of the midreservoir area took place during late September, and by October the entire reservoir was well mixed. Dissolved oxygen concentrations were near saturation levels for the rest of the year.

Definite seasonal variation in turbidity occurred. Surface turbidity was highest (maximum of 79 JTU during February at Station 4) during the winter and spring, when high rainfall, runoff, and erosion resulted in large amounts of suspended sediments in the lake. Inorganic suspended sediments persisted in the bottom zone of the lake throughout summer. Turbidity was lowest during fall, when

Table 2. Percentage fish catch (adjusted to 12-h set) by station and season in Ruth Reservoir, June 1974 through May 1975.

Season, and samples per station	Station	Species						Total
		Humboldt sucker	Golden shiner	Brown bullhead	White catfish	Rainbow trout	Largemouth bass	
Summer								
7	1	17	7	< 1	11	38	0	10
7	2	8	7	1	23	0	0	6
7	3	13	6	< 1	23	13	18	8
7	4	32	26	32	26	25	18	30
7	5	31	54	66	17	25	64	47
Fall°								
7	1	21	8	6	41	11	25	15
7	2	19	2	10	33	11	25	13
7	3	19	31	3	7	33	0	18
7	4	41	60	81	19	45	50	55
Winter°								
6	1	25	9	18	100	0	0	19
6	2	3	0	3	0	0	0	2
6	3	15	4	6	0	0	100	10
6	4	57	98	74	0	100	0	70
Spring								
6	1	1	0	0	13	0	0	1
6	2	4	7	5	26	0	0	7
6	3	11	0	5	26	0	0	6
6	4	22	77	39	30	0	0	52
6	5	62	16	52	4	0	0	34

°Catches at Station 5 were excluded because this lake area was dry in fall and winter.

all suspended sediments had been flushed from the reservoir. Turbidity was highest at the bottom and lowest at the surface during all seasons. Lake area effects also introduced considerable variation in turbidity—i.e., spatial trends in turbidity occurred as storm runoff moved through the reservoir.

Conductivity varied with time and with vertical and horizontal lake area. However, variation was not great, the values ranging only from 80 to 200 μmho/cm (mean, about 125 μmho/cm).

Simple and Multiple Linear Correlations

Correlations between fish catch and concurrent measurements of environmental variables at specified stations indicated that temperature and turbidity had major effects on fish catches (Table 5). Consistent significant direct temperature and inverse turbidity relationships with the catches of Humboldt sucker, brown bullhead, white catfish, and total species occurred.

Although a significant inverse relationship existed between fish catches and DO, there was no discernible biological basis for a cause-effect relationship of this type; i.e., increased DO concentrations would not be expected to cause a decrease in fish catches. The range of DO saturation variation was not great, and DO concentrations measured at the water depths of net sets were not limiting to fish. Since there was generally a high correlation ($r \geq 0.90$) between temperature and DO concentration, it is reasonable to assume that the fish-DO correlation is a result of the indirect temperature effect. Conductivity and fish catches were not consistently related.

Environmental variables with biologically explainable effects on fish catch were included in multiple linear correlations with fish catch (Table 6). Significant ($P < 0.01$) multiple linear correlations existed between total and individual species catch and the turbidity-temperature environmental system. Surface turbidity and bottom temperature accounted for 80.5 percent of the variation in total fish catch. Time of year, depth of sampling station, and Mad River inflow explained very little additional variation in total fish catch. This pattern was consistent for all major fish species. Turbidity and temperature accounted for 72.2, 53.5, and 58.8 percent of the catch variation for Humboldt suckers, brown bullheads, and white catfish, respectively. A significant ($P < 0.05$) relationship also existed between the turbidity-temperature system and the catch of golden shiners. However, the proportion of catch variation explained by temperature and turbidity—about 30 percent—was substantially less for the golden shiner than for the other species. In all tests, inclusion of additional environmental variables did not account for a statistically significant proportion of independent variation. The catches of largemouth bass and rainbow trout were so small that correlation analyses would not be meaningful.

Discussion

The fish population dynamics of the reservoir have not been continuously monitored since the dam was completed in 1961. However, current evidence does suggest that establishment of nonnative species in the late 1960s was associated with a decline in the rainbow trout population. Introductions of the golden shiner, brown bullhead, white catfish, and largemouth bass were unauthorized. Golden shiners were first observed during

Table 3. Gill net catches (adjusted to 12-h set) at Station 5 during summer-fall (s-f) and winter-spring (w-s) in Ruth Reservoir June 1974 through May 1975.

Species, and seasonal period	Number of sets	Catch	
		Total	Mean
Humboldt sucker			
s-f	10	223	22.3
w-s	9	171	19.0
Golden shiner			
s-f	10	429	42.9
w-s	9	45	5.0
Brown bullhead			
s-f	10	305	30.5
w-s	9	12	1.3
White catfish			
s-f	10	9	0.9
w-s	9	1	0.1
Total			
s-f	10	978	97.8
w-s	9	233	25.9

summer and fall 1968 (La Faunce 1968), and brown bullhead and white catfish during fall 1968. Largemouth bass are believed to have been introduced later—possibly in 1970. Changes in relative abundance of adult fish of different species are apparent from comparisons of gill net samples taken in 1968 with those taken during the present study. Rainbow trout composed 31 percent of the catch in 1968, but less than 1 percent in 1974–1975. The relatively high trout catch in 1968 probably represents a population that remained from the stocking of hatchery-reared fish in the previous May and the resident river population entrapped by the dam. Corresponding to the dramatic difference in trout catches were the substantial differences in catches of golden shiners (from 15 to 33 percent), brown bullheads (from 0 to 20 percent), and white catfish (from a trace to 3 percent). Humboldt suckers made up 54 percent of the catch in 1968 and 43 percent in 1974–1975. The largemouth bass maintains a naturally reproducing population and supports a sizable fishery in the reservoir. It was probably more abundant in 1974–1975 than the gill net samples indicated (<1 percent) because centrarchids are typically difficult to capture in nets. Crayfish, which were very abundant in the 1968 sample, were present only in trace amounts in 1974–1975.

Western suckers and golden shiners are two of the most successful competitors of rainbow trout in terms of reduced trout production in California reservoirs (Inland Fisheries Branch 1971). Humboldt sucker and golden shiner composed over 75 percent of the sample in numbers and 83 percent in weight during 1974–1975. Thus, the 1974–1975 species composition and relative abundance of nongame fish in Ruth Reservoir could have been a factor detrimental to the reservoir trout population. Erman (1973) reported that populations of (*Catostomus tahoensis*) and (*C. platyrhynchus*) in Sagehen Creek increased from 17.8 percent (1952–1961) before impoundment to 41.3 percent in Stampede Reservoir and 79.2 percent upstream (1970–1972) after impoundment. This illustrates that this stream-reservoir system favored sucker populations.

Since Humboldt suckers spawn in the Mad River during the same (spring) season as rainbow trout, it is likely that the young of the two species compete for space and food. At present, the natural reproduction of trout in the Mad River above Ruth Reservoir appears negligible.

The rainbow trout fishery of the reservoir has been maintained by stocking fingerling (1962–1968) and catchable-size fish (1969–1975). Since these hatchery-raised trout compete unsuccessfully with other reservoir species, the recent strategy of stocking catchable trout during times of heavy angler effort (i.e., before the opening weekend of the fishing season and before holidays) on a put-and-take basis is logical. However, if trout of a more predaceous strain were planted at a larger size, they would be able to forage on golden shiners.

Both temporal availability and spatial distribution of the fish in Ruth Reservoir were associated with environmental properties that varied on a seasonal basis. A cyclic trend of high catches during the warm summer and fall, and low catches during the cold and rainy winter and spring was apparent for all species. The environmental-fish relationships quantified during this study were simple; i.e., temperature was directly related, and turbidity inversely, to fish catches. Both temper-

Table 4. Mean seasonal environmental measurements at 1m below the surfaces (S), mid-depth (M), and 1m above the bottom (B) at Stations 1–4 in Ruth Reservoir, June 1974 through May 1975.

	Temperature (C)			Turbidity (JTU)			Conductivity (µmho/cm at 25 C)			Dissolved oxygen (mg/l)		
Season	S	M	B	S	M	B	S	M	B	S	M	B
Summer	22.2	18.3	14.8.	14.8	21.9	41.8	101.9	99.7	97.3	10.0	9.0	8.0
Fall	16.5	16.1	15.6	5.7	6.0	8.2	146.8	145.2	142.2	9.5	8.9	7.9
Winter	4.6	4.4	4.6	30.5	34.1	39.9	133.4	131.3	126.4	13.1	13.0	12.8
Spring	8.6	7.8	7.2	27.6	29.4	34.5	165.4	108.0	115.8	12.2	12.1	12.0
Annual mean	13.0	11.7	10.6	19.7	22.9	31.1	136.9	121.1	120.4	11.2	10.8	10.2

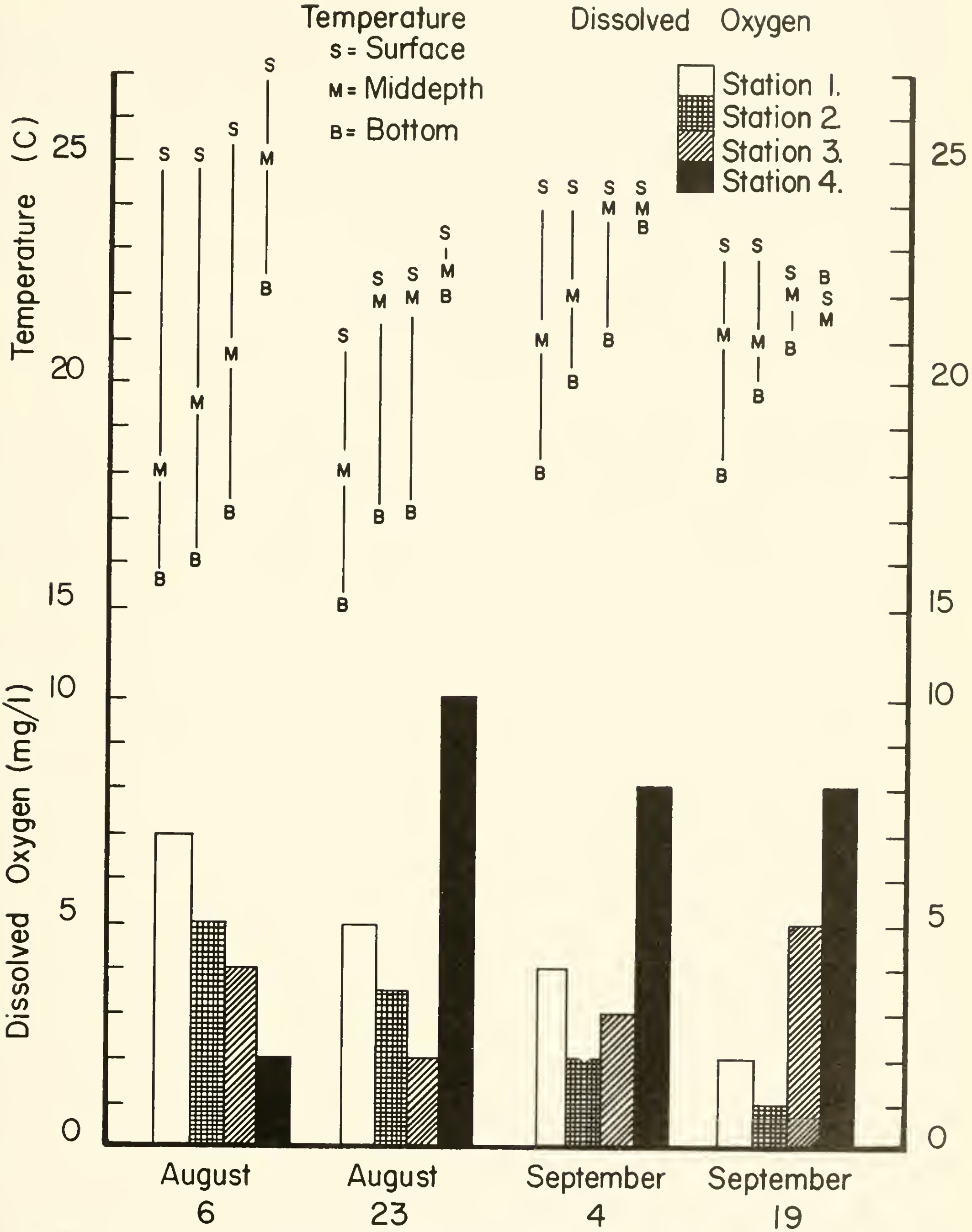


Fig. 4. Bottom-dissolved oxygen concentration and vertical temperature profile by station in Ruth Reservoir, August and September 1974.

ature and turbidity have known biological relationships affecting the survival, physiology, and behavior of fish.

The mean summer temperature in Ruth Reservoir (22.2 C) approximates the preferred temperature of the two most abundant fish species—Humboldt sucker and golden shiner (Reutter and Herdendorf 1974). The maximum surface temperature of Ruth Reservoir (27 C) exceeds the upper lethal threshold

TABLE 5. Significant correlation coefficients between fish catch and selected environmental variables measured at surface (S), mid-depth (M), and Bottom (B) at Stations 1–4 in Ruth Reservoir from June 1974 through May 1975 (26 observations per station, n = 104).

	Temperature			Turbidity		
Species	S	M	B	S	M	B
Rainbow trout						
Largemouth bass	.213°	.272°°	.311°°	–.214°	–.271°°	–.202°
Humboldt sucker	.381°°	.436°°	.477°°	–.383°°	–.400°°	–.369°°
Golden shiner		.214°	.276°°	–.201°	–.233°	–.269°°
Brown bullhead	.269°°	.347°°	.417°°		–.215°	–.243°
White catfish	.411°°	.460°°	.482°°	–.323°°	–.360°°	–.289°°
Total catch	.343°°	.431°°	.519°°	–.350°°	–.391°°	–.421°°

°P<0.05
°°P<0.01

of rainbow trout (National Academy of Sciences 1972); thus, the summer temperature regime restricts the spatial distribution of the trout. All other species, however, are capable of inhabiting the productive littoral and surface waters during the entire growing season. In fact, higher temperatures than those in Ruth Reservoir would favor largemouth bass and catfish, since their temperature for optimum growth exceeds 27 C (Strawn 1961, Andrews and Stickney 1972, Kilambi et al. 1970, Crawshaw 1975).

The linear area sampling design provided a description of the fish species habitat preference in relation to seasonal environmental dynamics. The relatively shallow upper end provides most of Ruth Reservoir's littoral area, and the river-reservoir interface. It represents an important habitat for the adult fish population, and probably serves as a spawning and nursery area. Humboldt sucker and golden shiner primarily inhabited this region, regardless of season. Brown bullhead likewise preferred this habitat during all seasons; however, the relative proportion of this species in the upper end of the reservoir increased during the summer. The relation between higher catches and the warm upper reservoir area indicates an interaction with temperature, since the upper end was the first to warm during spring and remained the warmest area of the lake throughout summer.

Turbidity and the associated high inflow-outflow were inversely related to fish catch; the behavior and distribution of all fish species were negatively influenced by turbid water. Turbidity, inflow, outflow, flushing rate, and water level are all closely interrelated in Ruth Reservoir. Water level fluctuations affect the reproductive success of reservoir-spawning fish such as largemouth bass, white catfish, brown bullhead, and golden shiners in terms of spawning habitat, nursery habitat, and food availability. Drawdowns resulting in elimination of the shoals during the spawning season can cause direct mortality to eggs and larvae. Since larvae and juvenile fish feed on zooplankton, an abundant population of zooplankton is necessary at the time fish eggs hatch. Lider (1977) documented the depleting effect of the flushing rate on zooplankton populations in Ruth Reservoir; appreciable populations did not develop during spring until surface spilling ended. Young fish can also be lost in the discharge of a reservoir. Walberg (1971) reported that the timing and rate of flushing affects the year-class survival of reservoir fish.

In addition to biological parameters, inflow and outflow play a major role in the development of water quality patterns within a reservoir (Wunderlich 1971). Therefore, factors that alter the flow regime—downstream water needs, modification of the dam, or modification of the outlet structure, would affect the biotic and abiotic ecosystem of Ruth Reservoir.

SUMMARY AND CONCLUSIONS

The fish population of Ruth Reservoir was dominated by Humboldt sucker, golden shiner, and brown bullhead. White catfish formed an appreciable proportion of the population. Although largemouth bass were not heavily represented in the catch, their population is naturally maintained and their actual abundance is probably substantial. The species

Table 5 continued.

Conductivity			Dissolved oxgyen			Sampling period	Sampling station
S	M	B	S	M	B		
			–.283°°	–.247°		–.195°	
.213°	.214°		–.393°°	–.469°°	–.376°°	–.406°°	.307°°
			–.256°°	–.198°			.365°°
			–.261°°	–.195°	–.230°		.320°°
			–.496°°	–.453°°	–.415°°	–.248°	
.210°	.231°	.203°	–.436°°	–.398°°	–.320°°	–.223°	.443°°

composition and relative abundance of the Ruth Reservoir fish population is not conducive to salmonid production. The rainbow trout population is negligible and maintained by put-and-take stocking. Catch of all fish species was positively correlated with temperature and negatively correlated with turbidity and inflow-outflow. Management practices affecting these environmental parameters would thus effect the fish population of Ruth Reservoir.

We believe the following measures would be beneficial in the management of the Ruth Reservoir fishery:

1. Promote the Ictalurid fishery, including night fishing.
2. Continue stocking catchable-size rainbow trout during times of high angler effort. Study the feasibility of stocking more predacious salmonids (e.g., steelhead, *Salmo gairdneri,* or brown trout, *Salmo trutta*) at a larger size.
3. Study the detailed ecology of the largemouth bass population.
4. Study the spawning potential for salmonids in the upper Mad River.
5. Undertake watershed management in the upper Mad River to alleviate soil erosion and the associated turbidity problems.

Literature Cited

Andrews, J. W., and R. R. Stickney. 1972. Interaction of feeding rates and environmental temperature on growth, food conversion, and body composition of channel catfish. Amer. Fish. Soc., Trans. 101(1):94–99.

California Department of Water Resources. Reservoir limnology, Ruth Reservoir, 1969. Northern District. Red Bluff, California (unpublished data).

Cooley, W. W., and P. R. Lohnes. 1971. Multivariate Data Analysis. John Wiley and Sons, New York. 380 pp.

Crawshaw, L. I. 1975. Attainment of the final thermal preferendum in brown bullheads acclimated to different temperatures. Comp. Biochem. Physiol. A. Comp. Physiol. 52(1):171–173.

Erman, D. C. 1973. Upstream changes in fish populations following impoundment of Sagehen Creek, California. Trans. Amer. Fish. Soc. 102(3):626–629.

Inland Fisheries Branch. 1971. Report on the status of reservoir research. California Dept. of Fish and Game. Inland Fish. Admin. Rep. 71-1. 45 pp.

Iwatsubo, R. T., L. T. Britton, and R. C. Averett. 1972. Selected physical and chemical characteristics of 20 California lakes. U.S. Dept. Inter. Geol. Surv. Menlo Park, California. 59 pp.

Kilambi, R. W., J. R. Noble, and C. E. Hoffman. 1970. Influence of temperature and photoperiod on growth, food consumption, and food conversion efficiency of channel catfish. Pages 519–531 *in* Proc. Southern Div. American Fish. Soc., Atlanta, Georgia.

La Faunce, D. A. 1968. Gill net sampling at Ruth Lake, Trinity County. California Dept. of Fish and Game. Eureka, California (unpublished mimeo). 2 pp.

Lider, E. L. 1977. The distribution and abundance of plankton and their association with environmental variables in Ruth Reservoir, California. Unpublished thesis. Humboldt State Univ., Arcata, California. 88 pp.

National Academy of Sciences. 1972. Water quality criteria 1972. U.S. Environ. Prot. Agency. 594 pp.

Reutter, J. M., and C. E. Herdendorf. 1974. Laboratory estimates of the seasonal final temperature preferenda of some Lake Erie fish. Proc. Conf. Great Lakes Res. (Int. Assoc. Great Lakes Res.) 17:59–67.

Sokal, R. R., and J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 pp.

Strawn, K. 1961. Growth of largemouth bass fry at various temperatures. Trans. Amer. Fish. Soc. 90:334–335.

TABLE 6. Multiple linear correlations between fish catch and turbidity and temperature at Σ Stations 1–4 in Ruth Reservoir from June 1974 through May 1975 (n = 26).

Species	Environmental variables	Correlation coefficients (r)	r^2	Multiple correlation coefficient (R)	R^2	F for analysis of variance on R
Humboldt sucker	Surface turbidity	-.759°°	.576	.849°°	.727	29.809°°°
	Bottom temperature	.814°°	.663			
Brown bullhead	Surface turbidity	-.579°°	.335	.731°°	.535	13.228°°°
	Bottom temperature	.728°°	.530			
White catfish	Surface turbidity	-.586°°	.343	.767°°	.588	16.439°°°
	Bottom temperature	.766°°	.587			
Golden shiner	Surface turbidity	-.547°°	.299	.549°	.301	4.963°
	Discharge temperature	.450°	.203			
Total	Surface turbidity	-.835°°	.697	.897°°°	.805	47.535°°°
	Bottom temperature	.833°°	.694			

°$P < 0.05$
°°$P < 0.01$
°°°$P < 0.001$

U.S. ARMY CORPS OF ENGINEERS. 1973. Draft environmental impact statement Butler Valley Dam and Blue Lake Project. San Francisco District, Corps of Engineers. 211 pp.

VIGG, S. 1979. Distribution and relative abundance of fish in Ruth Reservoir, California, in relation to environmental parameters. Unpublished thesis. Humboldt State Univ., Arcata, California. 70 pp.

WALBURG, C. H. 1971. Loss of young fish in reservoir discharge and year-class survival, Lewis and Clark Lake, Missouri River. Pages 441–448 *in* G. E. Hall, ed., Reservoir fisheries and limnology. Spec. Publ. No. 8. Amer. Fish. Soc., Washington, D.C.

WINZLER AND KELLY. 1975. Ruth Lake Reservoir turbidity study. Winzler and Kelly, Environmental Consultants, Eureka, California. 27 pp.

WUNDERLICH, W. O. 1971. The dynamics of density stratified reservoirs. Pages 219–231 *in* G. E. Hall, ed., Reservoir fisheries and limnology. Spec. Publ. No. 8. Amer. Fish. Soc., Washington, D.C.

YOUNG, J. C. 1971. Geology of the Mad River Basin. Pages 27–32 *in* Proceedings of the Mad River Symposium sponsored by the Office of Dean of Public Services and Department of Geology and Earth Science. Humboldt State College, Arcata, California.

TEMPERATURE AND SALINITY RELATIONSHIPS OF THE NEVADAN RELICT DACE

Steven Vigg[1]

Abstract.— The relict dace, *Relictus solitarius*, represents the only genus and species of fish native to Ruby, Butte, Goshute, and Steptoe valleys in northeastern Nevada. In their natural habitats temperature ranges 0–25 C and salinity 175–1,158 mg/liter. The upper median thermal tolerance limit (96-hr TL50) of Butte Valley relict dace was 30.6 C when acclimated at 18–20 C. Relict dace tolerated total dissolved solids (TDS) of 11,043 mg/liter with no mortality during 96-hr exposures, but experienced 100 percent mortality at concentrations of 15,759 mg/liter with a mean resistance time of 23 hours. Tolerance of relict dace to 30 C was lowered as TDS was increased from 2,845 to 5,652 mg/liter. The Butte Valley fish were slightly more resistant to elevated salinities than the Goshute Valley sample, and conversely the Goshute Valley sample may be slightly more resistant to elevated temperature.

The relict dace, *Relictus solitarius*, is listed as "of special concern" by the Endangered Species Committee of the American Fisheries Society (Deacon et al. 1979). However, it was recently taken off the State of Nevada's protected species list.

Before the present study there were no quantitative data on the habitat requirements of relict dace. The purpose of this research was to determine a provisional upper lethal temperature limit (96-hr TL50), and to conduct range finding tests on the total dissolved solids (TDS) tolerance of this unique fish.

Relict dace apparently evolved during the past 1.5 to 2.0 million years in the contiguous drainage basins of pluvial lakes Franklin, Gale, Waring, and Steptoe just south of the conjoining parts of the Lahontan and Bonneville basins (Hubbs et al. 1974). As these Pleistocene lakes desiccated over the last 10,000 years, the relict dace was the only genus and species of fish to survive in the remnant springs of contemporary Ruby, Butte, Goshute, and Steptoe valleys, which comprise some 14,682 km^2 in northeastern Nevada. The species also occurs in Spring Valley, where it is believed to be an introduction (Fig. 1).

The taxon was first described by Hubbs and Miller (1972) from extensive research dating back to 1934. As well as being morphologically distinct from its closest relatives, *Gila* and *Rhinichthys*, this endemic cyprinid is also unique in terms of genetics (Lugaski 1980) and geographical distribution (Smith 1978).

Relict dace was once the most abundant of the four fish species native to the north central Great Basin (Hubbs et al. 1974). The species is losing populations and habitat (Hardy 1979), due to predation and competition by exotic fish species, modification of natural springs into stock ponds and irrigation channels, and groundwater mining.

Methods

Temperature and salinity bioassays were conducted on relict dace from November 1980 to March 1981. Test fish were transported from their natural habitats in Ruby, Butte, and Goshute valleys (Fig. 1) to the Desert Research Institute (DRI) Bioresources Center laboratory in Reno. Upon arrival at DRI the fish were maintained in 425-liter holding tanks a minimum of four days for observation of handling stress. During this time the fish were acclimated at 18–20 C in dechlorinated Truckee River water prior to testing.

Relict dace from three different sources (Franklin Lake, Atwood Ranch, and Phalan Spring) were tested for 96 hours over a temperature range of 29.0 to 34.3 C. Two replicates of five fish each were tested in static 19-liter aquaria for each treatment. The test

---

[1] Bioresources Center, Desert Research Institute, P.O. Box 60220, Reno, Nevada 89506.

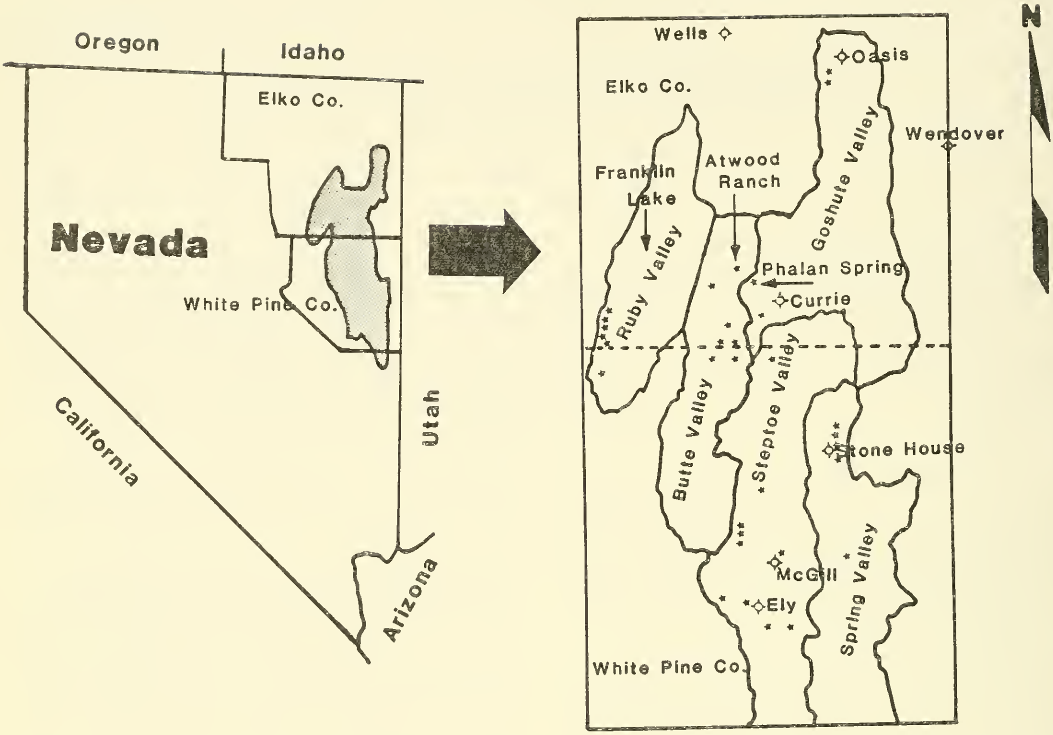

Oregon
Idaho
Elko Co.
Nevada
White Pine Co.
California
Utah
Arizona
Wells
Oasis
Elko Co.
Wendover
Franklin Lake
Atwood Ranch
Goshute Valley
Ruby Valley
Phalan Spring
Currie
Butte Valley
Steptoe Valley
Stone House
McGill
Ely
Spring Valley
White Pine Co.
N

Fig. 1. Areal distribution of relict dace in five valleys in northeastern Nevada. The shaded area indicates known distribution of relict dace. Arrows mark the location of habitats where fish were collected. Asterisks (*) identify relict dace habitats documented by Hubbs et al. (1974).

aquaria were placed in a thermostatically controlled water bath to maintain a constant temperature (± 0.1 C). Five control fish were placed in dechlorinated Truckee River water in a 19-liter aquarium at room temperature (approximately 20 C) for each treatment; no control fish died.

Table 1. Salinity related measurements of test media for TDS-alkalinity bioassays with relict dace, *Relictus solitarius*.

Test media	TDS* (mg/ℓ)	Total alkalinity (mg/ℓ)	Specific conductance (µmhos/cm at 25 C)	pH
Truckee River	157	78	187	7.5
½ Pyramid Lake ½ Distilled	2,845	639	4,730	9.2
1X Pyramid Lake	5,652	1,262	8,560	9.2
2X Pyramid Lake	11,043	2,580	16,900	9.2
3X Pyramid Lake	15,759	3,670	22,900	9.2
4X Pyramid Lake	20,475	4,620	28,200	9.1

*Summation of all constituents.

Test fish were not fed 24 hours prior to the bioassay nor during the tests. Dissolved oxygen (DO) and pH were measured at least once and usually three times daily. The aquaria were continuously aerated, and mean DO values always exceeded 6 mg/liter. Temperature was measured with a calibrated digital thermometer at least three times daily in each aquarium.

Range finding tests were conducted to determine the TDS-alkalinity tolerance of relict dace. Concentrated Pyramid Lake water (2X, 3X, 4X) was used to achieve elevated salinity levels (Table 1). Fish were derived from two sources, Atwood Ranch Spring and Phalan Spring, to test for differences by population. Procedures similar to those of the thermal bioassays were used: replicates of five fish/test in 19-liter continuously aerated aquaria with selected environmental parameters monitored. Temperature was held constant (21.4–22.3 C) via the thermal water bath. Data were interpreted in terms of resistance time as well as mortality.

Another series of tests was performed to evaluate salinity-temperature interactions, utilizing only the Atwood Ranch Spring population. Pyramid Lake water (1X), and ½ Pyramid – ½ distilled water were utilized as the test media for normal ($\simeq$21–22 C) and elevated ($\simeq$30 C) temperatures. For all salinity tests, Truckee River water (low TDS) was used for controls. Electrical conductivity and alkalinity determinations for each treatment were determined by the DRI water chemistry lab, using standard analytical procedures (APHA et al. 1975). TDS was determined by summation of all measured constituents.

The total and mean weight of each group of five test fish were determined (in water) to the nearest 0.1 gram prior to testing. Dead fish were immediately removed and preserved in 10 percent formalin; time of each death was recorded. The criteria for death were no opercular movements and no response to touch. Statistical analyses were conducted utilizing programs from SPSS (Nie et al. 1975).

RESULTS

Temperature

Range finding tests were conducted on relict dace from Franklin Lake in the Ruby Valley. No mortality occurred at 29.0 C during 96 hours, and 100 percent mortality occurred at 34.3 C within 27 hours (10 fish/test). More definitive results were derived from the Butte Valley (Atwood Ranch) population with four replicate tests over a range of 30–31 C (Table 2). The 96-hr median tolerance limit (TL50) for relict dace collected at the Atwood Ranch Spring was 30.6 C.

Concurrent tests on relict dace from Atwood Ranch and Phalan Spring at 30.7 C indicated that the latter population may be slightly more resistant to high temperatures. The Phalan Spring population experienced only 40 percent mortality at 30.7 C, but the Atwood Ranch Spring fish suffered 80 percent mortality. The higher temperature tolerance of the Phalan Spring population may be due to the long-term physiological acclimatization at 19.5–23 C compared to 16.5–21 C at the Atwood Ranch Spring (Table 3).

TDS-Alkalinity

Relict dace tolerated total alkalinity ($HCO_3^- + CO_3^=$ as $CaCO_3$) and corresponding TDS of 2,580 mg/liter and 11,043 mg/liter, respectively, for 96 hours without experiencing any mortality (Table 4). TDS levels of 15,759 and 20,475 mg/liter resulted in 100 percent mortality of both populations of relict dace tested. Analysis of variance illustrated a significant difference in resistance times by concentrations ($P<0.001$), fish population ($P<0.05$), and interaction between

Table 2. Temperature tolerance tests (96-hr) of Butte Valley relict dace (*Relictus solitarius*) conducted from November 1980 to March 1981 in dechlorinated Truckee River water at mean acclimation temperatures of 18–20 C. Sample size is five fish per test in replicate tests.

	Mean chemical characteristics			Fish		
Mean test temperature (C)	Number of measurements	Dissolved oxygen (mg/*l*)	pH	Mean weight (g)	Number dead (96 hr)	Percent mortality (10 fish)
30.0	9	6.4	8.75	1.82	0	0
30.0	”	6.5	8.20	1.46	0	
Control (21.6)	”	7.3	8.50	2.14	0	
30.6	8	6.8	8.76	2.08	2	50
30.6	”	6.8	8.17	2.40	3	
Control (22.7)	”	7.6	7.98	1.62	0	
30.7	18	6.5	8.54	2.24	4	80
30.7	”	6.6	8.36	2.28	4	
Control (21.3)	”	7.6	8.15	2.08	0	
31.0	7	6.1	8.39	1.68	5	100
31.1	”	6.1	8.51	3.20	5	
Control (21.7)	”	7.3	8.03	1.70	0	

the main effects ($P<0.001$). An a-posteriori comparison showed that the Butte Valley (Atwood Ranch) fish were significantly more resistant to concentrated alkaline-saline waters than the Goshute Valley (Phalan Spring) population ($P<0.05$). The resistance of time of Atwood Ranch fish was about twice that of the Phalan Spring fish at both the 15,759 and 20,475 mg/liter levels (Table 5).

There exists an apparent interaction between temperature and salinity tolerances of relict dace (Table 4). No mortality occurred at low temperatures (21–22 C) over a range of TDS from 157 to 5652 mg/liter. But at an elevated temperature (30 C) differential mortality occurred: 0, 20, and 60 percent at TDS levels of 157, 2845, and 5652 mg/liter, respectively.

DISCUSSION

Temperature

Compared to other families of freshwater fishes, the Cyprinidae generally occupy an intermediate rank of upper thermal tolerance. Through acclimation, an upper lethal temperature exceeding 30 C is achieved by most cyprinids; at the highest tested acclimation levels eight species ranged from 29.3 (*Rhinichthys atratulus*) to 38.6 C (*Carrassius auratus*) (Brett 1956).

The upper lethal TL50 of 30.6 C herein determined for relict dace acclimated at 18–20 C falls within the range exhibited by other cyprinids. If the test fish were acclimated to higher temperatures, it is likely that the upper lethal temperature would be significantly greater.

The maximum water temperature I measured in a relict dace habitat was only 23 C; however, Hubbs et al. (1974) recorded summer temperatures as high as 25 C. Different populations of relict dace are subjected to a wide variety of temperature regimes. Nonthermal springs and shallow ponds may have great daily and seasonal changes with minimum temperatures near freezing (e.g., Franklin Lake). At the other end of the spectrum are thermal springs that never vary more than a few degrees in terms of diel, seasonal, and annual, presumably over extremely long time periods. For example, the head of Phalan Spring exhibited less than a 1 C diel change in February when air temperature ranged from 7.5 to -9.0 C, and seasonal water temperature variation was only about 3 C. In addition, there are various types of intermediate gradations with respect to the temperature emanating from the springs and

TABLE 3. Environmental characteristics of selected relict dace, *Relictus solitarius*, habitats, April 1980–February 1981.

Valley/Site	Date	Temperature (°C)	Total dissolved solids (mg/ℓ) Summation of all constituents	Total dissolved solids (mg/ℓ) Summation (USGS 1979)	Total alkalinity (mg/ℓ $CaCO_3$)
Ruby					
Alkali Pond	12/80	2.0	1721	1157.8	912
Franklin Lake	12/80	3.5	683.8	444.3	387
Steptoe					
Steptoe Ranch	12/80	20.8	388.5	255.6	215
Cardano Ranch	12/80	11.5	415	265.3	242
Goshute					
Phalan Spring	04/80°	22	–	216	115
	07/80°	23	–	175	118
	09/80°	22	–	190	132
Butte					
Atwood Ranch	04/80°	19	–	375	172
	07/80°	21	–	325	182
	09/80°	20	–	325	158
	12/80	16.5	469.3	325.7	232
Odgers	04/80°	12	–	216	120
	07/80°	20	–	205	115
	09/80°	14	–	190	118

°Conducted by: Water Analysis and Consulting, Inc. 1980. Water Quality Study Wells Environmental Statement Area. Bureau of Land Management, Elko District.

the changes that occur in the length of streams and/or depths of ponds.

Limited data exist on thermal tolerance levels of cyprinid species inhabiting the Great Basin. Speckled dace (*Rhinichthys osculus*) taken from intermittant Arizona streams at < 25 C had ultimate incipient upper lethal levels of 33 C for juveniles and 32 C for adults (John 1964). The Borax Lake chub, *Gila boraxobius,* is endemic to a thermal lake in southeastern Oregon; the lake typically exhibits temperatures of 29–32 C, with extremes of 17–35 C (Williams and Williams 1980). Another cyprinid from the northwestern Great Basin, the desert dace (*Eremichthys acros*), is endemic to thermal springs ranging from 18.5–40.5 C; this Nevada species tolerated temperatures of 2–37 C in the laboratory when acclimated at 23 C (Nyquist 1963). Virgin River spinedace (*Lepidomeda mollipinis*), native to the Colorado River System, had a 14-hr upper lethal temperature of 31.2–31.4 C when acclimated at 20 C (Espinosa and Deacon 1978).

In contrast, extensive research has been done on the thermal requirements of Cyprinodontidae inhabiting the Death Valley region of the southern Great Basin. Pupfish (*Cyprinodon*) acclimated at 10–20 C can tolerate temperatures of 39–40 C (Brown and Feldmeth 1971, Otto and Gerking 1973, Feldmeth et al. 1974).

Representatives of another cyprinodont genus (*Crenichthys*) are remnants of Pluvial river systems in the southeastern Great Basin. *Crenichthys baileyi* inhabits springs in the Moapa Valley at constant temperatures of 32.2 C (Kopec 1949). In the Moapa River *C. baileyi* and *Moapa cariacea* (Cyprinidae) occupied habitats at temperatures of 27–32 C and 19.5–32 C, respectively (Deacon and Bradley 1972). *Crenichthys baileyi* and *C. nevadae* live in various spring outflows in the White River Valley and Railroad Valley, respectively, at temperatures ranging from 21 to 37.3 C (Hubbs et al. 1967). At Lockes Ranch spring complex *C. nevadae* were observed at temperatures of 18.3–37.8 C (Baugh and Brown 1980).

Although individuals may survive for short periods of time at extremely high temperatures, the maximum constant temperature occupied by a reproducing population of desert fish is rarely greater than 35 C (Soltz and Naiman 1978). This may be attributed to the differential tolerance of various life stages; e.g., Amargosa pupfish (*Cyprinodon nevadensis*) juveniles are most tolerant of extreme temperatures, with adults intermediate, and eggs least tolerant (Shrode 1975, Shrode and Gerking 1977). The reproductive tolerance range (≤50 percent hatch) of *C. nevadensis* was 24–30 C or one-seventh the critical thermal tolerance range (Shrode

TABLE 4. Salinity tolerance tests (96 hr) of relict dace *Relictus solitarius*, conducted during December 1980 and March 1981. The first series of bioassays tests interaction with temperature; the second series tests differences by fish population. Sample size is five fish per test.

		Mean chemical characteristics				Fish		
TDS (mg/*l*)	Population: valley (habitat)	Number of measurements	Temperature (C)	D.O. (mg/*l*)	pH	Mean weight (g)	Number dead	Percent mortality
157 (Control)	Butte (Atwood)	9	21.6	7.3	8.50	2.14	0	0
	”	”	30.0	6.4	8.75	1.82	0	
	”	”	30.0	6.5	8.20	1.46	0	
2,845	Butte (Atwood)	”	21.9	7.4	9.11	1.78	0	0
	”	”	30.0	6.4	9.20	1.18	1	20
5,652	Butte (Atwood)	”	20.9	7.3	9.21	1.60	0	0
	”	”	29.9	6.4	9.20	2.22	3	60
11,043	Butte (Atwood)	12	21.4	7.6	9.24	2.14	0	0
	Goshute (Phalan)	”	21.4	7.6	9.24	2.00	0	0
15,759	Butte (Atwood)	7	21.8	7.6	9.25	2.22	5	100
	Goshute (Phalan)	4	22.0	7.4	9.13	1.92	5	100
20,475	Butte (Atwood)	2	22.3	7.1	9.09	1.90	5	100
	Goshute (Phalan)	”	22.3	7.1	9.09	1.80	5	100
157 (Control)	Butte (Atwood)	12	21.4	7.6	8.35	1.98	0	0
	Goshute (Phalan)	”	21.4	7.6	8.30	6.02	0	

and Gerking 1977). This example illustrates that multiple criteria are necessary to establish the thermal requirements of a fish species. Thus, the TL50 determined in this study at a single acclimation regime is a useful baseline datum but is not comprehensive.

TDS-Alkalinity

The relict dace has experienced a variable environment during the past two million years in the Great Basin. Numerous cycles of Pluvial filling and interpluvial desiccation of large Pleistocene lakes occurred. Concomitant changes in the salinity of the lacustrine habitats undoubtedly took place. The variable content of TDS presumably has been a factor of considerable importance in the survival or extinction, and probably in the speciation of the populations of endemic fishes (Hubbs et al. 1974). During the past 10,000 years the lacustrine habitats of the relict dace have completely dried up and the species persists in remnant springs. The vast reduction of surface water to isolated springs is the outstanding feature of the habitats of native fishes in the Great Basin (Hubbs et al. 1974).

The elevated salinity level that relict dace tolerated (11,043 mg/liter TDS) is over six times the maximum TDS level of any current relict dace habitat measured. The corresponding total alkalinity level (2,580 mg/liter) represents nearly three times that in any current habitats. The spring habitats are generally <250 mg/liter total alkalinity and <500 mg/liter TDS (Table 3); the most saline habitats are ponds in the Ruby Valley, which exhibit total alkalinity levels as high as 912 mg/liter (TDS = 1,721 mg/liter). I hypothesize that relict dace evolved the physiological mechanisms to withstand highly saline-alkaline waters during the desiccation of their lacustrine environment.

TABLE 5. Mean resistance time of Atwood Ranch (A) and Phalan Spring (P) relict dace, *Relictus solitarius*, to highly alkaline-saline waters. Sample size is five fish per test.

TDS (mg/*l*)	Population	Mean resistance time (minutes)	95% confidence interval (minutes)
11,043	A	Indefinite (>5760)	—
	P	Indefinite (>5760)	—
15,759	A	1907	1204–2610
	P	848	280–1416
20,475	A	213	121–305
	P	111	70–152

In contrast to relict dace habitats, Cyprinodont environments in the southern Great Basin can be extremely saline—as much as 4.5 times that of sea water, composed predominantly of NaCl (Hunt et al. 1966). The composition of one saline habitat, Cottonball Marsh, was about 78 percent NaCl, with alkalinity not listed as a constituent (LaBounty and Deacon 1972). During laboratory studies with the ionic composition approximating that of sea water, the Cottonball Marsh pupfish (*Cyprinodon milleri*) survived at 88,000 mg/liter TDS, with a few individuals tolerating 130,000 mg/liter for several weeks (Naiman et al. 1976). Numerous field observations of various *Cyprinodon* species living at salinities greater than 90,000 mg/liter are documented in the literature (Barlow 1958, Deacon and Minckley 1974).

Thus, relict dace can tolerate only a fraction of the TDS at which Cyprinodonts exist. This is probably a reflection of the differences in their respective evolutionary environments. Precursors of the Cyprinodontidae had marine affinities (Smith 1981), and the family is apparently preadapted to harsh physical and chemical conditions; this enabled the group to further evolve tolerance to extremes of salinity and temperature (Miller 1981). In contrast, Cyprinidae is a primary freshwater family (Miller 1958). However, the ionic composition of their present environments and test media may also be a critical factor; i.e., the alkalinity component could affect the TDS tolerance of both taxa.

Salinity bioassays on relict dace at normal and elevated temperatures demonstrated a synergistic effect. Brett (1960) points out that with the multiple role of temperature bringing increased attention to the problem of interaction, emphasis will shift away from the singular effects of temperature to synergistic effects within the overall characteristics of environments that permit survival of the species. In his work with the euryplastic *Cyprinodon macularius*, Kinne (1960) showed that the combination of temperature and salinity was of basic physiological importance; the effects of a given temperature depend on the salinity and vice versa. Similarly, when dealing with the habitat requirements of relict dace, the synergistic relationships of salinity and temperature are important with respect to their physiology and ecology.

ACKNOWLEDGMENTS

This research was sponsored by the Desert Research Institute (DRI) Project Assignment Committee. Dr. Clifford J. Murino, DRI president, was very supportive of the work. Consultation with Dr. James E. Deacon (University of Nevada, Las Vegas) was helpful in initiating this research on relict dace. Dr. Robert R. Miller (University of Michigan, Ann Arbor) kindly reviewed my proposal and manuscript for accuracy of content. Mr. David L. Galat (Colorado Cooperative Fishery Research Unit) and Dr. Thomas P. Lugaski (University of Nevada, Reno) critically read the manuscript and made helpful suggestions. DRI Water Center Analytical Laboratory conducted water chemical analyses.

LITERATURE CITED

APHA (AMERICAN PUBLIC HEALTH ASSOCIATION), AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater, 14th ed. New York, New York, USA. 1193 pp.

BARLOW, G. W. 1958. High salinity mortality of desert pupfish, *Cyprinodon macularis*. Copeia. 1958:231-232.

BAUGH, T. M., AND B. G. BROWN. 1980. Field observations on the response of the Railroad Valley springfish (*Crenichthys nevadae*) to temperature. Great Basin Nat. 40(4):359-360.

BRETT, J. R. 1956. Some principles in the thermal requirements of fishes. Quart. Rev. Biol. 31(2):75-87.

———. 1960. Thermal requirements of fish—three decades of study. Pages 110-117 *in* C. M. Tarzwell, ed., Biological problems of water pollution. United States Department of Health, Education, and Welfare. Robert A. Taft Sanitary Engineering Center, Cincinnati, Ohio, USA.

BROWN, J. H., AND C. R. FELDMETH. 1971. Evolution in constant and fluctuating environments: thermal tolerances of desert pupfish (*Cyprinodon*). Evolution. 25(2):390-398.

DEACON, J. E., AND W. G. BRADLEY. 1972. Ecological distribution of fishes of Moapa (Muddy) River in Clark County, Nevada. Trans. American Fisheries Soc. 101(3):408-419.

DEACON, J. E., G. KOBETICH, J. D. WILLIAMS, AND S. CONTRERAS. 1979. Fishes of North America endangered, threatened, or of special concern. Fisheries (Bethesda) 4(2):29-44.

DEACON, J. E., AND W. L. MINCKLEY. 1974. Desert fishes. Pages 385-487 *in* Desert Biology, Vol. 2. G. W. Brown, Jr., ed. Academic Press, New York, New York, USA.

ESPINOSA, F. A., AND J. E. DEACON. 1978. Rearing bait fish in the desert southwest. State of Nevada. Final Report to Federal Aid in Commercial Fisheries Research and Development Project No. 6-9-D. University of Nevada, Las Vegas. USA. 29 pp.

FELDMETH, C. R., E. A. STONE, AND J. H. BROWN. 1974. An increased scope for thermal tolerance upon acclimating pupfish (*Cyprinodon*) to cycling temperatures. J. Comp. Physiol. 89:39-44.

HARDY, T. 1979. The Inter-Basin Area Report—1979. United States Department of the Interior and the State of Nevada. Pages 5-21 *in* Proceedings of the Desert Fishes Council. Vol. XI. Bishop, California, USA.

HUBBS, C., R. C. BAIRD, AND J. W. GERALD. 1967. Effects of dissolved oxygen concentration and light intensity on activity cycles of fishes inhabiting warm springs. Am. Midl. Nat. 77(1):104-115.

HUBBS, C. L., AND R. R. MILLER. 1972. Diagnosis of new cyprinid fishes of isolated waters of the Great Basin of western North America. Trans. San Diego Soc. Nat. Hist. 17(8):101-106.

HUBBS, C. L., R. R. MILLER, AND L. C. HUBBS. 1974. Hydrographic history and relict fishes of the north central Great Basin. Mem. California Acad. Sci. Vol. 7. 259 pp.

HUNT, C. B., T. W. ROBINSON, W. A. BOWLES, AND A. L. WASHBURN. 1966. Hydrologic basin, Death Valley, California. U.S. Geol. Surv. Prof. Paper No. 494-B.

JOHN, K. R. 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. Ecology. 45:112-119.

KINNE, O. 1960. Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiol. Zool. 33(4):288-317.

KOPEC, J. A. 1949. Ecology, breeding habits, and young stages of Crenichthys baileyi, a cyprinodont fish of Nevada. Copeia 1949(1):56-61.

LABOUNTY, J. F., AND J. E. DEACON. 1972. *Cyprinodon milleri*, a new species of pupfish (family Cyprinodontidae) from Death Valley, California. Copeia 1972(4):769-780.

LUGASKI, T. P. 1980. Comparative chemotaxonomy of selected Great Basin native cyprinid fishes. Unpublished dissertation. Univ. of Nevada, Reno, USA.

MILLER, R. R. 1958. Origin and affinities of the freshwater fish fauna of western North America. Pages 187-222 *in* Carl L. Hubbs, ed., Zoogeography. American Association for the Advancement of Science, Baltimore, Publ. No. 51.

———. 1981. Coevolution of deserts and pupfishes (Genus Cyprinodon) in the American Southwest. Pages 39-94 *in* R. J. Naiman and D. L. Soltz, eds., Fishes in North American deserts. Wiley & Sons, New York, New York, USA.

Naiman, R. J., S. B. Gerking, and R. E. Stuart. 1976. Osmoregulation in the Death Valley pupfish *Cyprinodon milleri* (Pisces: Cyprinodontidae). Copeia 1976(4):807–810.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. A. Bent. 1975. Statistical package for the social sciences, 2d ed. McGraw-Hill, New York, New York, USA.

Nyquist, D. 1963. The ecology of *Eremichthys acros*, an endemic thermal species of cyprinid fish from northwestern Nevada. Unpublished thesis. Univ. of Nevada, Reno, USA.

Otto, R. G., and S. D. Gerking. 1973. Heat tolerance of a Death Valley pupfish (Genus *Cyprinodon*). Physiol. Zool. 46(1):43–49.

Shrode, J. B. 1975. Developmental temperature tolerance of a Death Valley pupfish (*Cyprinodon nevadensis*). Physiol. Zool. 48:378–389.

Shrode, J. B., and S. D. Gerking. 1977. Effects of constant and fluctuating temperatures on reproductive performance of a desert pupfish, *Cyprinodon n. nevadensis*. Physiol. Zool. 50(1):1–10.

Smith, G. R. 1978. Biogeography of intermountain fishes. Intermountain biogeography: a symposium. Great Basin Nat. Mem. No. 2:17–42.

Smith, M. L. 1981. Late Cenozoic fishes in warm deserts of North America: a reinterpretation of desert adaptations. Pages 11–38 *in* R. J. Naimann and D. L. Soltz, eds., Fishes in North American deserts. Wiley & Sons, New York, New York, USA.

Soltz, D. L., and R. J. Naiman. 1978. The natural history of native fishes in the Death Valley system. Natural History Museum of Los Angeles County, Science Series 30:1–76.

USGS (United States Geological Survey). 1979. Techniques of water-resources investigations of the United States Geological Survey. Chapter A1. Methods for determination of inorganic substances in water and fluvial sediments (M. W. Skougstad, M. J. Fishman, L. C. Friedman, D. E. Erdmann, and S. S. Duncan, eds.) Book 5, Laboratory Analysis.

Water Analysis & Consulting, Inc. 1980. Water quality study, Wells environmental statement area. Conducted for Bureau of Land Management, Elko District Office. 27 pp.

Williams, J. E., and C. D. Williams. 1980. Feeding ecology of *Gila boraxobius* (Osteichthyes: Cyprinidae) endemic to a thermal lake in southern Oregon. Great Basin Nat. 40(2):101–114.

OBSERVATIONS ON WOUNDFIN SPAWNING AND GROWTH IN AN OUTDOOR EXPERIMENTAL STREAM

Paul Greger[1] and James E. Deacon[1]

Abstract.— The response of woundfin to different substrates and current speeds was investigated in an outdoor experimental stream. Fish spawned in groups of 15–20 over 5–10 cm rock substrate in a .06 to .09 m/sec current at a depth of 10 cm. Eggs were adhesive on the undersides of the rocks. Fish spawned under these conditions grew to approximately 55–60 mm TL in 5 months.

The woundfin minnow, *Plagopterus argentissimus* Cope, is an endangered cyprinid presently occurring only in the Virgin River system of Nevada, Arizona, and Utah. Recent attempts at reestablishing this species in other areas of its original range in the Gila River Basin of Arizona have been unsuccessful. Almost 70 percent of the original woundfin habitat in the Virgin River has been rendered unreliable during part of the year by irrigation diversions (Deacon 1979). A variety of development projects involving modification of present river flows pose additional threats to the continued survival of the woundfin.

This study was undertaken to help identify habitat requirements for successful spawning. Such information is essential to an analysis of probable environmental impacts of various proposed development projects on the Virgin River as well as to the selection of areas within the former range of the species that might be suitable for reintroduction. Data on growth rates was taken to aid in an interpretation of a large data base on length-frequency of woundfin in the Virgin River.

Methods and Materials

Approximately 50 adult woundfin were collected from the Virgin River near the inflow of Beaver Dam Wash at Littlefield, Arizona, on 26 April 1980 and transported to the experimental stream facility on the University of Nevada campus in Las Vegas, Nevada. Many of the adults were robust, appearing in prime reproductive condition. Fish were immediately transferred to the stream facility upon arrival.

The stream (Fig. 1) consists of two raceway sections, a narrow upper section and a wider lower section, both constructed of concrete. Two pools, 2 × 2 m with a maximum depth of 1 m connect the raceways. The upper raceway is approximately 7 m in length and 45 cm in width, with a maximum depth of 15 cm. The lower raceway is 7 m in length and 90 cm in width, with a maximum depth of 45 cm. Current is generated by a 115 volt, 6.7 amp centrifugal pump that draws water out from the west pool through a circular rock filter. Water is pumped into the top end of the upper raceway, flows into the east pool, and then through the lower raceway into the west pool.

No filters were used to remove waste products but fresh well water was added daily to replace seepage and evaporation. This, in combination with low fish densities, seemed sufficient to prevent accumulation of ammonia or other harmful substances. The system design provides a choice of current speeds in the upper raceway as indicated for an average water level in Figure 1. Current speed in the lower raceway was too slow to measure with a Marsh McBirney hand-held, paramagnetic current meter.

We provided a choice of substrates by placing large rock (15–25 cm diameter), small rock (5–10 cm diameter), gravel, and sand in distinct segments in both raceways (Fig. 1). Daily observations of woundfin dis-

---

[1] Department of Biological Sciences, University of Nevada, Las Vegas, Nevada 89154.

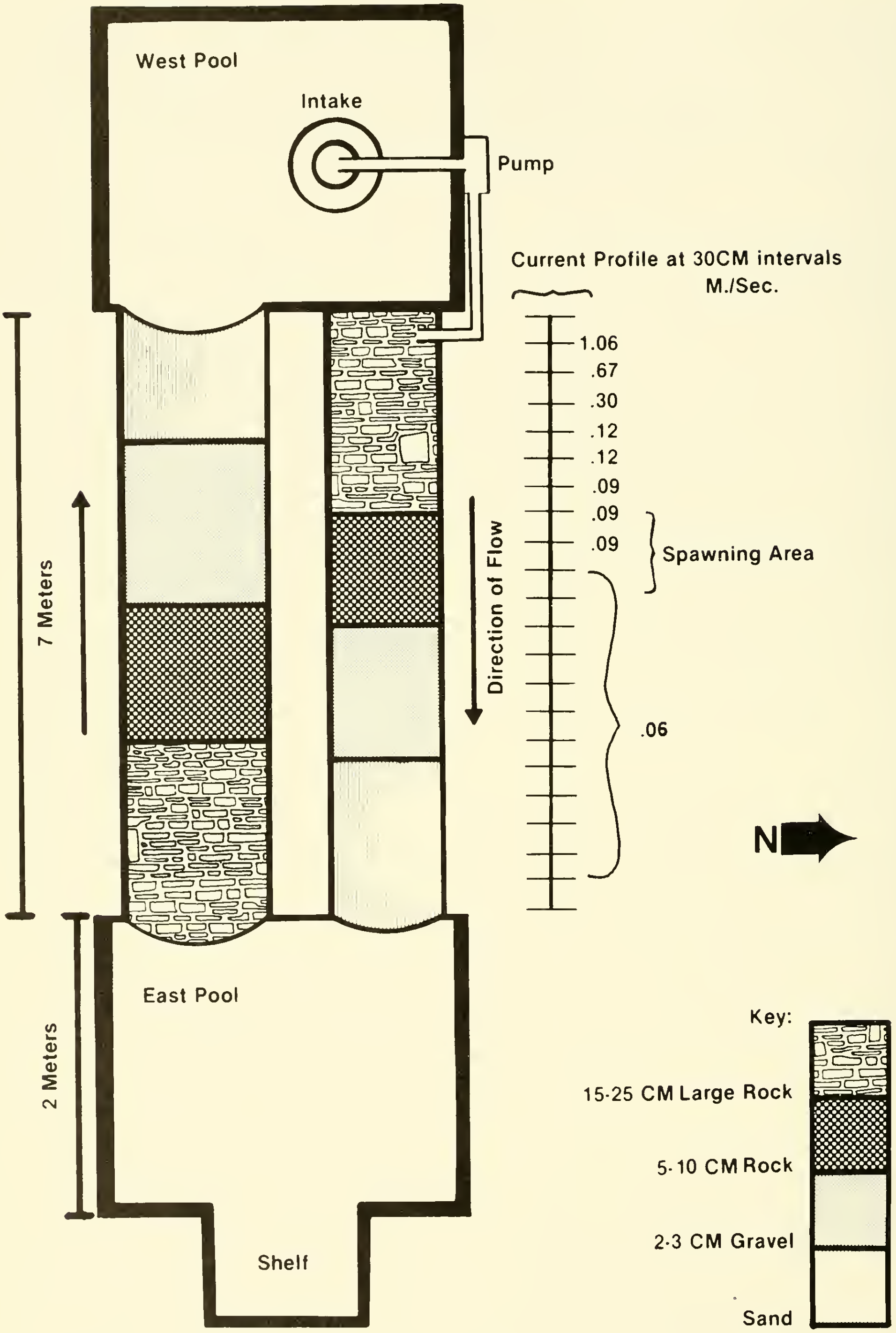

West Pool
Intake
Pump
Current Profile at 30CM intervals
M./Sec.
1.06
.67
.30
.12
.12
.09
.09
.09
Spawning Area
.06
Direction of Flow
7 Meters
2 Meters
N
East Pool
Shelf
Key:
15-25 CM Large Rock
5-10 CM Rock
2-3 CM Gravel
Sand

Fig. 1. Outdoor experimental stream at the University of Nevada, Las Vegas.

tribution and behavior in the stream system were made. Water temperature was measured with a mercury thermometer and a Ryan thermograph. Fish were collected, preserved, and measured at intervals to document growth rates of fry and fingerlings.

Collections are on deposit in the Museum of Natural History at UNLV.

Results and Discussion

Fish were placed in the experimental stream on 26 April 1980 and observed at irregular times each day. They usually occupied the deeper waters in the pools and swam in loosely organized schools. On 3 May a tightly packed wedge-shaped school of 15–20 adults was observed making many quick turns over the small rock (5–10 cm) substrate of the upper raceway where the current speed was .06–.09 m/sec and depth was 7–10 cm. The distinctive movements of this group were essentially confined to this 45 cm section and continued for about 40 minutes. Similar movements were noted on occasions over the next 9 days. These subsequent occasions involved 4–7 fish and lasted only 4–5 minutes. Water temperature was 25 C during each spawning event and fluctuated from 19 to 26 C during the period of spawning.

Spawning movements involved quick movements of the tightly packed school over the small rock substrate. Occasional flashing occurred, and at irregular intervals one or a few fish would leave the group and swim downstream to the pool below. Similarly at irregular intervals one or a few fish would swim upstream from the pool below to join the group. When fish entered the school, the group frequently would become more compact and appear to stop and vibrate as a group around the new arrival. This was assumed to be the spawning act. Immediately following it, the fish-to-fish distance would increase slightly, some individuals would pick at the substrate, and the main group would continue its tight circling movements over the small rock substrate. Although sex was not determined, we presumed that mature males dominated the school and that the fish entering and leaving were largely mature females.

Depth was uniform throughout the upper raceway. Current speeds of .06–.09 m/sec occurred over small rock, gravel, and sand substrates. Spawning activity was confined to the small rock substrate, where adhesive eggs were dropped between the interstices of the 5–10 cm rock.

Woundfin fry were first observed in the stream on 14 May. All fry were located in the lower section of the stream where currents were minimal (.01–.03 m/sec). Woundfin fry appeared to orient close to the edges of the raceway where current speed was slower or over a shallow shelf in one end of a pool. They did not occur over the deep water. The fry, when first observed on 14 May, were about 8–10 mm TL. Water temperature was about 20 C.

Close examination of the presumed spawning site on 15 and 17 May revealed adhesive eggs attached to the underside of the 5–10 cm rock in the upper raceway. This was further evidence that woundfin utilized the small rock substrate for spawning. Eggs were approximately 1.5 mm in diameter and had a brown center with a clear outer region. Some eggs were white and opaque. If a spawn did occur on 3 May 1980, the period of development is about 10–11 days. Data for other cyprinids is similar. For example, *Rhinchthys osculus* in the Chiricahua Mountains in Arizona required 6 days for hatching at 18 C plus 7–8 days to swim up from the interstices of the gravel (John 1963).

Fry of 9 mm total length were first observed to orient in current (.06 m/sec) over sand in the upper raceway on 15 May. These fry held position close to the bottom and edges of the raceway in slower currents. Fry also apparently selected areas of shade in the late afternoon. On 18 May woundfin fry appeared to be increasing their range of movements to include rock and sand substrates in the upper raceway. From 22 May to 12 June fry (10–13 mm) moved further upstream over gravel and rock substrates until by 24 June, 18.5 mm fish were observed moving over all substrates in the upper raceway. As woundfin increase in size, they develop an increasing ability to move into swifter waters. This suggests that in the environment woundfin of 18–20 mm total length are able to move away from areas with slow current into open water areas where current is moderate. Field observations are consistent with these data.

On 4 July the first schooling activity of fingerling was noted in the east pool. Some chasing behavior of fingerlings by adult woundfin was also observed. Finally, on 8 July, the stream was partially drained and about 100 woundfin fingerling were removed and transported to the National Endangered Species Hatchery at Dexter, New Mexico. Twenty-five woundfin were retained for further study of growth. Over the previous month, mortality related to an *Ichthyophthirius* infection had been substantial.

Information on growth of woundfin is given in Table 1. The first three weeks of the experimental period show little or no change in mean size. In fact, week 3 shows a slightly lower mean length than the previous week. This could have resulted from a second spawning or it could signal a difficult transition from yolk-dependent growth to food-dependent growth.

Weeks 4 and 5 show a growth increment of about 2 mm per week. Weeks 5, 6, and 7 show approximate growth increments of 4 and 5 mm per week. Thereafter, monthly measurements (July, August, and September) show growth changes of 12.4, 15.1, and 5.6 mm, respectively. Woundfin hatched in early May had reached a mean length of 35.7 mm by the end of July, 50.8 mm by the end of August, and 56.4 mm by 25 September. Observations were terminated on 25 September.

The stream was colonized by aquatic plants (*Chara* sp. and *Naja* sp.) and by a variety of macroinvertebrates (Ostracoda, Chydoridae, Chironomidae, Ephemeroptera, Anisoptera, and Coleoptera). Although a high protein commercial feed was supplied, it appeared that woundfin fry fed primarily on the natural foods present. These included Chironomid adults, pupae, and larvae and Chydorid crustaceans. Fry appeared to be in good condition.

TABLE 1. Weekly growth of woundfin fry and fingerling in an outdoor experimental stream. The mean length represents the average of all measurements made during the weekly period.

Week	Date	N	x̄ Length (mm)	Range (mm)
1	14–20 May	31	9.4	8.5–11.5
2	21–27 May	51	9.9	7.5–12.0
3	29 May–4 June	15	9.2	7.0–11.0
4	12 June	7	12.7	9.0–15.0
5	15–17 June	9	14.3	12.0–16.0
6	25 June	6	18.5	17.0–20.0
7	1 July	7	23.3	21.0–25.0
11	27 July	14	35.7	32.0–39.0
14	30 August	7	50.8	48 –55.0
17	25 September	8	56.4	49 –61.0

CONCLUSIONS

1. A small rock (5–10 cm diameter) substrate was specifically selected as the spawning substrate.
2. Spawning was accomplished when a gravid female joined a group of ripe males exhibiting spawning behavior over the proper substrate (depth was about 7–10 cm).
3. Woundfin eggs are adhesive and drop between the interstices of rocks, where they adhere to the underside.
4. Spawning of woundfin occurs primarily in the spring when water temperatures reach about 25–26 C during the diurnal temperature cycle.
5. Woundfin of 10–12 mm TL are restricted in their movements by current, but woundfin of 17.0–20 mm TL are able to move freely throughout the stream in a variety of current speeds.
6. Woundfin grow to about 50 mm in four months, a mean growth rate of about three mm/week. Growth may then slow, but an average size of 55–60 mm during the first growing season is not unlikely.

ACKNOWLEDGMENTS

Thom Hardy assisted in collection, transportation, and observation of woundfin. Tina Hardy assisted in maintenance of the stream and with observations of the fish. Their enthusiastic cooperation is much appreciated. This study was supported in part by Contract 14-16-0002-78-919 from the U.S. Fish and Wildlife Service. Permits were provided by the Arizona, Nevada, and Utah Fish and Game departments and by the U.S. Fish and Wildlife Service.

LITERATURE CITED

DEACON, J. E. 1979. Endangered and threatened fishes of the west. Great Basin Nat. Mem. No. 3:41–64.

JOHN, K. R. 1963. The effect of torrential rains on the reproductive cycle of *Rhinichthys osculus* in the Chiricahua Mountains, Arizona. Copeia 1963(2):286–291.

EARLY DEVELOPMENT OF THE RAZORBACK SUCKER, *XYRAUCHEN TEXANUS* (ABBOTT)

W. L. Minckley[1] and Eric S. Gustafson[1]

ABSTRACT.— Fertilized ova of razorback sucker, *Xyrauchen texanus*, were adhesive for 3 to 4 hours after fertilization. Cleavage was completed at 24 hours, gastrulation occurred at 34 hours, and blood circulation was established at 117 hours. Hatching occurred from 5.2 to 5.5 days after fertilization. Larvae were from 6.8 to 7.3 mm TL at hatching. Yolk was assimilated at 13 days (10 mm TL). All fins were formed and had ossified rays at 64 days (27 mm TL). The unique nuchal keel appeared about 200 days after fertilization.

The razorback sucker, *Xyrauchen texanus* (Abbott), is endemic to the Colorado River basin. As with much of the southwestern ichthyofauna (Pister 1981), it is declining in abundance (Minckley 1983). A program was commenced in 1974 to develop means of propagating the species (Toney 1974) and to delineate certain aspects of its life history. We studied embryological, larval, and juvenile development of the species in 1974–75. Although our data are somewhat outdated in light of recent studies of catostomid larvae (reviewed by Fuiman and Witman 1979), almost nothing has appeared on the early life history of this unique species. Winn and Miller (1954) presented a key to postlarval fishes of the lower Colorado River basin that included photographs and some descriptions of young *X. texanus*. A photograph by Douglas (1952: Fig. 3) was reidentified by Winn and Miller as speckled dace (*Rhinichthys osculus* [Girard]) rather than *X. texanus*. The present paper thus describes and figures early life-history stages of the razorback sucker as determined from hatchery-and laboratory-reared individuals.

METHODS

Initial information on hatchery propagation and rearing of razorback suckers originated from adult fish seined near Cottonwood Cove in Lake Mohave, Arizona-Nevada, in winter 1974, and was compiled by personnel at Willow Beach National Fish Hatchery (in part, Toney 1974). Eggs were stripped from females and fertilized, and developing young were initially housed in an indoor raceway at a mean water temperature of 14 C, then transferred 13 days posthatching to an outdoor raceway where water temperature averaged 15 C. Samples were preserved daily in 10 percent formalin during the first month, and intermittently thereafter. Late postlarval and juvenile phases described below are based on the 1974 cohort.

Additional adults were trammel netted from below Hoover Dam and in the vicinity of Carp Cove in Lake Mohave in March–April 1975. Most males were in active spawning condition, but females were either spent or not yet mature. Suitable females were interperitonealy injected with human chorionic gonadotropin, which induced oocyte maturation. A few hours after injection about 5,000 eggs were stripped from a single female and immediately fertilized with sperm of two males, as has been observed in nature (Douglas 1952). It is notable that water-hardened eggs obtained from naturally-matured females in 1974 were 2.9 mm diameter, but comparable ova obtained from hormone-induced maturation were 1.8 mm diameter. This disparity is far greater than has before been recorded in catostomid ova diameters (Fuiman and Trojnar 1980). We assume it resulted from precipitous maturation after hormone injection, but have no further explanation. By the time of hatching, both sets of embryos were of comparable length.

---

[1] Department of Zoology, Arizona State University, Tempe, Arizona 85287.

Developing embryos were maintained in an indoor raceway at Willow Beach for 28 hours at temperatures ranging from 13 to 17 C. Eggs were then transported to aquaria at Arizona State University, where development continued at a constant temperature of 20 C. Observations and measurements were recorded from living specimens by a stereomicroscope equipped with ocular micrometer and camera lucida, and with a range of magnification of 2 to 2,000 X. All measurements are of total length.

Observations on the 1975 cohort were made hourly through the first 30 hours, then every 2 hours until after hatching. Illustrations of selected stages through prolarval development were prepared through use of a camera lucida and from photographs. Ovum through prolarval development presented here is thus based on the 1975 fish. Specimens were preserved periodically in acetoformalic acid (AFA; 9.0 parts ethanol, 0.4 parts 40 percent formaldehyde, and 0.5 parts glacial acetic acid). When larvae began to swim and feed actively, samples were preserved less frequently.

Development of the razorback sucker was divided into four major phases as defined by Hubbs (1943): (1) embryological development, fertilization of the egg until hatching; (2) prolarval development, hatching to absorption of yolk; (3) postlarval development, yolk absorption to ossification of pelvic fin-rays; and, (4) juvenile development, pelvic ray ossification to maturation of gonads. Development staging followed Balinsky's (1948) general pattern for cyprinid fishes. Descriptive terminology was derived from Ryder (1885), Stewart (1926), Tavolga (1949), Winn and Miller (1954), and Long and Ballard (1976).

Results

Embryological Development

Stage 1: unfertilized egg; day 0, 0 hour, 1.5 mm diameter. Ova milky white and translucent.

Stage 2: fertilized egg; day 1, 1 hour, 1.8 mm diameter. Chorion transparent and yolk milky-white and translucent; animal pole not yet visible to unaided eye. Water-hardened eggs with greater specific gravity than water, ova demersal, chorion adhesive, ova adhering to substrate and one another.

Stage 3: 2 blastomeres, 3 hours (Fig. 1A); beginning of cleavage. Blastomeres transparent, approximately 0.5 mm total diameter. Animal and vegetal poles distinguishable to unaided eye; ova telolecithal, cleavage meroblastic. Ova no longer adhesive. AFA preservation causes animal cells to whiten and become opaque; yolk becomes yellow white; chorion remains transparent.

Stage 4: 4 blastomeres, 5 hours; second cleavage. Blastomeres approximately 1.0 mm total diameter.

Stage 5: 8 blastomeres, 6 hours; third cleavage. Blastomeres occupy 1.2- by 0.8-mm rectangle on animal pole.

Stage 6: 16 blastomeres, 7 hours; fourth cleavage.

Stage 7: 32 blastomeres, 9 hours; fifth cleavage (Fig. 1B).

Stage 8: 64 blastomeres, 10 hours; sixth cleavage. 128 blastomeres, 11 hours; seventh cleavage. Large-celled blastula (morula); no blastocoel. Blastomeres occupy 25 percent of yolk surface.

Stage 9: small-celled blastula (morula), 14 hours. Individual cells distinguishable; blastomeres bulging upward from round yolk mass, occupying 25 percent of yolk surface. Blastomere layers progressively thinner toward periphery of blastoderm; no blastocoel.

Stage 10: morula, 24 hours (Fig. 1C). Individual cells indistinguishable except with high power and chorion removed; blastoderm with granular appearance; undersurface flat, lying on flattened surface of yolk sphere; no blastocoel. Cleavage terminated.

Stage 11: blastula (epiboly of blastoderm), day 2, 28 hours; 1.8 mm diameter (Fig. 1D). Blastoderm spreading over yolk sphere and thinning (blastodisc). Blastocoel present. Periblast visible as cellular rim along periphery of blastoderm, beginning formation of inner layer of yolk sac. Outer layer of yolk sac to be formed from epiblast derived from blastoderm. Blastoderm no longer bulging from yolk, capping under 33 percent of sphere.

Stage 12: early gastrula, 34 hours (Fig. 1E). Underrim of blastodisc thickened to form "*randwulst*" or marginal ridge with inner layer termed the germ ring. Ring thickest posteriorly, recognized as embryonic shield. Presumptive endodermal cells at posterior edge of shield beginning to involute through blastopore and spread beneath blastoderm. Cells of prechordal plate and notochord migrating inward over dorsal lip of blastopore (establishment of embryonic axis). Presumptive mesodermal cells also turning inward, positioned either side of embryonic axis beneath ectoderm and above endoderm. Periblast, *randwulst* cells, and germ ring cells not involved in involution spread over 50 percent of yolk sphere.

Stage 13: middle gastrula, 35 hours. Invagination lengthening embryonic shield; blastopore marks posterior axis of embryo.

Stage 14: late gastrula, 36 hours (Fig. 1F). Embryonic shield nearly reaching animal pole of egg on dorsal meridian; shield approximately 1.3 mm long; concentration of invaginated cells clearly visible at anterior end of shield; *randwulst* cells and germ ring cells, accompanied by presumptive ectodermal cells, forming outwardly as epiblast; marginal ridge shifted below equator of egg; uncovered portion of yolk protrudes as yolk plug.

Stage 15: early neurula, 45 hours, 1.8 mm diameter. Blastopore closed; yolk plug no longer protruding. Embryonic shield approximately 2.0 mm long, circumscribing 75 percent of egg, overlying yolk sac. Neural plate formed, lateral and anterior margins not clearly delimited. Notochord in form of ridge pressing into yolk, lateral notochord rudiment not clearly separated from sheets of mesoderm.

Stage 16: late neurula, 47 hours (Fig. 1G). Neural keel remains 2.0 mm long, circumscribing 75 percent of egg. Neural plate contracted, more defined along edges. Cephalic region arrow shaped in dorsal view; eye rudiments forming; neural ridges as folds on either side of neural plate. Notochord separated from mesoderm.

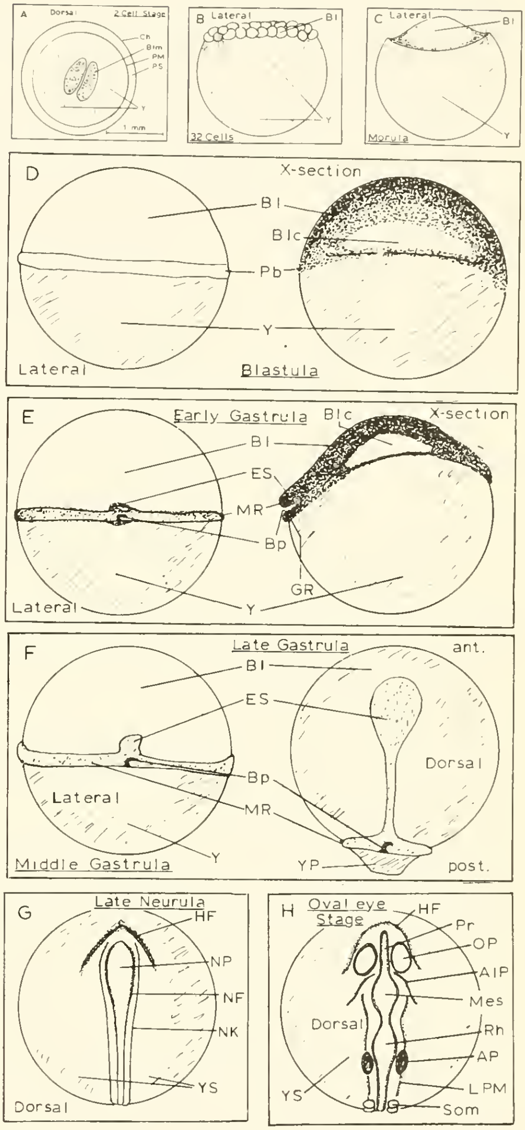

A
Dorsal
2 Cell Stage
Ch
Blm
PM
PS
Y
1 mm
B
Lateral
Bl
Y
32 Cells
C
Lateral
Bl
Y
Morula
D
X-section
Bl
Blc
Pb
Y
Lateral
Blastula
E
Early Gastrula
Blc
X-section
Bl
ES
MR
Bp
GR
Lateral
Y
F
Late Gastrula
ant.
Bl
ES
Dorsal
Bp
Lateral
MR
Middle Gastrula
Y
YP
post.
G
Late Neurula
HF
NP
NF
NK
YS
Dorsal
H
Oval eye Stage
HF
Pr
OP
AIP
Mes
Dorsal
Rh
AP
YS
LPM
Som

Fig. 1. Early embryological stages of razorback sucker, *Xyrauchen texanus*; chorion removed in all but A. Legend: AIP = anterior intestinal portal, Ant. = anterior, AP = auditory placode, BI = blastoderm, Blc = blastocoel, Blm = blastomere, Bp = blastopore, Ch = chorion, ES = embryonic shield, GR = germ ring, HF = head fold, LPM = lateral plate mesoderm, Mes = mesencephalon, MR = marginal ridge, NF = neural fold, NK = neural keel, NP = neural plate, OP = optic placode, Pb = periblast, PM = perivitelline membrane, PS = perivitelline space, Rh = rhombencephalon, som = somites, Y = yolk plug, and YS = yolk sac.

Stage 17: eye rudiments, day 3, 49 hours, embryo length 2.0 mm. Brain cavities and spinal cord formed by contraction of neural plate. Eye rudiments as lateral protrusions at anterior end of brain. Prosencephalon (forebrain), mesencephalon (midbrain) and rhombencephalon (hindbrain) distinguishable. Audi-

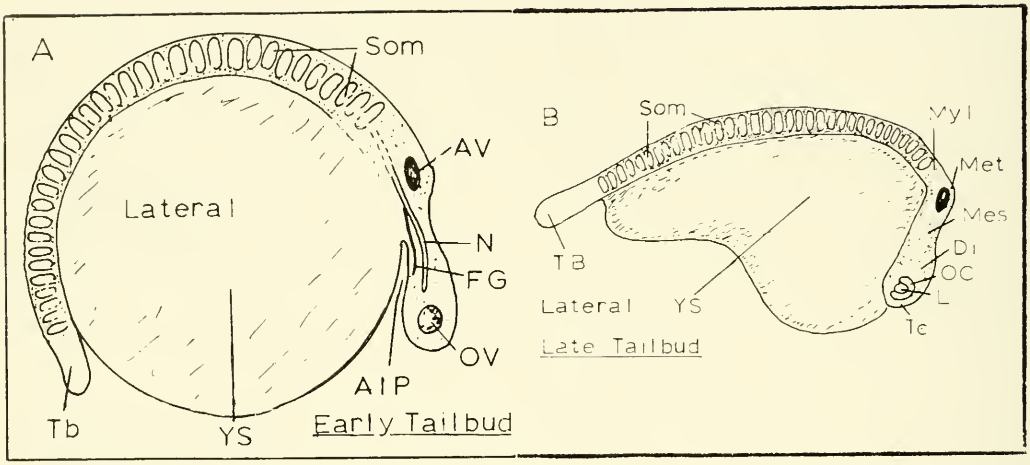


Fig. 2. Early (A) and late (B) tailbud embryological stages of razorback sucker, *Xyrauchen texanus*; chorion removed—embryo extended in "B." Legend as in Figure 1 when applicable, and AV = auditory vesicle, Di = diencephalon, FG = foregut, L = lens, Met = metencephalon, Myl = myelencephalon, N = notochord, OC = optic cup, OV = optic vesicle, TB = tailbud, and Te = telencephalon.

tory vesicles at level of hindbrain; first pair of somites present.

Stage 18: cavities in eye rudiments, 53 hours. Optic placodes elongated, containing narrow vesicles; head-fold visible; subcephalic pocket and anterior intestinal portal ventral to head. Auditory placodes formed; 14–16 pairs of somites.

Stage 19: oval eyes, 57 hours, 2.5 mm (Fig. 1H). Optic placodes rounded to oval; vesicles not yet present in auditory placodes; 30 pairs of somites. Tail process distinguishable.

Stage 20: early tailbud, 65 hours, 3.0 mm (Fig. 2A). Optic vesicles flattened on outer margins; lens forming. Auditory placodes with small vesicles. Tailbud developed, protruding from yolk sphere. Foregut forming.

Stage 21: late tailbud, day 4, 78 hours, 3.8 mm (Fig. 2B). Anterior portion of embryo (head and anterior trunk) overlying yolk sphere; posterior portion (posterior trunk and tail) overlying cylindrical yolk mass. Optic stalks, cups, and lenses distinguishable. Prosencephalon divided into telencephalon (future cerebrum) and diencephalon (future epithalamus, thalamus, and hypothalamus); rhombencephalon divided into metencephalon (future cerebellum) and myelencephalon (medulla oblongata). Heart rudiment present; tailbud lengthening, embryo motile within chorion.

Stage 22: heart beat, 83 hours, 4.0 mm. Heart pulsations noted. Tail at right angle to body axis. Kidney ducts (pronephric ducts) and dorsal aorta formed ventral to neural tube and notochord; alimentary tract lined by endoderm and nearly complete; stomadeum and proctodeum not apparent.

Stage 23: fin fold, day 5, 103 hours, 5.3 mm. Fin fold appearing on tail and posterior dorsum; head growing outward from yolk sac. Circulatory system formed; nasal placodes present; tail beginning to straighten.

Stage 24: blood circulation, 117 hours, 6.8 mm (Fig. 3). Head extending from yolk. Heart visible within pericardial cavity; flexed, sinus venosus and atrium lying above and left of ventricle and conus arteriosis; endocardium and epimyocardium distinguishable. Three visceral (gill) arches formed; pupils visible within eyes, brown pigment granules in choroid regions. Yolk reduced to cylinder below body axis. Blood flow: atrium → ventricle → conus arteriosus → ventral aorta → branchial afferents → branchial efferents → dorsal aorta and internal carotid arteries → vitelline artery → caudal vein → posterior cardinal vein → anterior cardinal and vitelline veins → common cardinal vein (Duct of Cuvier) → sinus venosus → atrium. Embryos extremely motile, some beginning to rupture chorion.

Stage 25: pectoral fin rudiments, 120 hours, 6.8 mm. Pectoral fin anlagen appearing posteriad and ventrad to auditory vesicles. Tail slightly upturned. Stomadeum

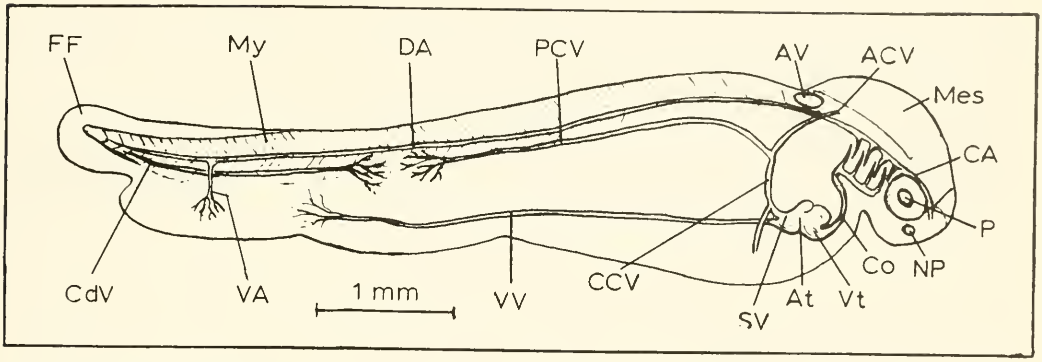


Fig. 3. Embryo of razorback sucker, *Xyrauchen texanus*, at initial circulation of blood; embryo extended and chorion not depicted. Legend as in Figures 1 and 2 when applicable, and ACV = anterior cardinal vein, At = atrium, CA = carotid artery, CCV = common cardinal vein (duct of Cuvier), CdV = caudal vein, Co = conus artriosus, DA = dorsal artery, FF = fin fold, My = myomeres, NP = nasal placode, P = pupil, PCV = posterior cardinal vein, SV = sinus venosus, VA = vitelline artery, Vt = ventricle, and VV = ventral vein.

clearly visible. Myotomes discernible above yolk. Embryos flex once every 12 to 13 heart beats.

Stage 26: pectoral fin buds, day 6, 125 hours, 7.3 mm. Rudiments of pectoral fins protrude, slightly flattened dorso-ventrally. Head continuing to extend outward from yolk.

Prolarval Development

Stage 27: hatching, 131 hours, 7.3 mm (Fig. 4). Pectoral fin buds paddle shaped. Tail straightened and median fin fold developed anteriorly on dorsum. Head flexed 45 degrees relative to body axis. Proctodeum discernible; eye pigment increased. Embryos scarcely motile, flexing along bottom with no directed movements.

Stage 28: 142 hours, 7.5 mm. Four gill arches visible; head remains at 45 degree angle to body axis. Pectoral fin buds thin and broadly rounded; ventral fin fold appearing behind proctodeum.

Stage 29: 144 hours, 7.5 mm. Lower jaw formed, not yet reaching level of eye; mouth oriface round. Head angle less than 45 degrees relative to body axis.

Stage 30: early prolarva, day 7, 162 hours, 8.0 mm (Fig. 5). Head straightened. Lower jaw reaching midlevel of eye, not movable. Pectoral fin differentiated into muscular lobe and membrane, not movable. Ventral fin fold developed to most anterior extension, embryonic fin membrane (continuous median fin) complete. Opercular membranes forming. Optic pigmentation brown, granular, almost complete; no other melanophores.

Stage 31: middle prolarva, day 9, 238 hours, 9.0 mm. Rudimentary gas bladder evident. Lower jaw to anterior border of eye, movable; mouth rounded and terminal. Opercle covers anteriormost gill. Pectoral fin 0.5 mm long, movable. Proctodeum yet

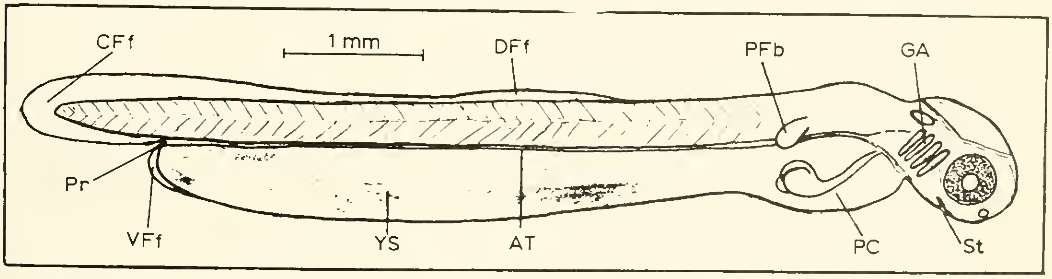


Fig. 4. Prolarva of razorback sucker, *Xyrauchen texanus*, at hatching; legend as in Figures 1 to 3 when applicable, and AT = alimentary tract, CFf = caudal fin-fold, DFf = dorsal fin-fold, GA = gill arches, PC = pericardial cavity, PFb = pectoral fin-bud, Pr = proctodeum, St = stomadeum, and VFf = ventral fin-fold.

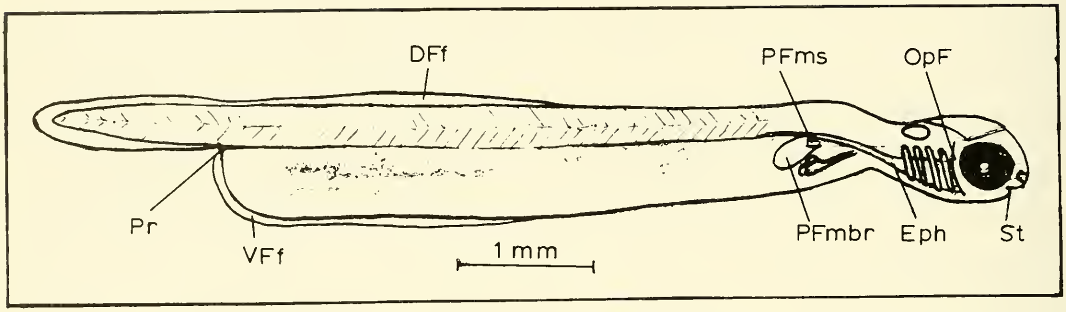


Fig. 5. Early prolarva of razorback sucker, *Xyrauchen texanus*; legend as in Figures 1 to 4 when applicable, and Eph = esophagus, OpF = opercular flap, Pfmbr = pectoral fin membrane, and PFms = pectoral fin musculature.

closed, yolk much reduced. Eye pigmentation completed, becoming black. Brown, stellate melanophores on ectoderm overlying mid- and hindbrain, and on paired dorsal pigment line, paired dorso-visceral pigment line (upper body cavity), and unpaired midventral pigment line. No melanophores on horizontal myoseptum. Larvae swim to surface and feed on ground aquarium fishfood (Tetramin^{R}). Resting heart rate 120 beats per minute.

Stage 32: late prolarva, day 10, 263 hours, 9.0 mm (Fig. 6). Liver reaching midventral line; yolk largely assimilated. Pectoral fins 0.8 mm long, no fin rays in any fin. Pigmentation increasing on dorsal, dorso-visceral, and midventral lines; melanophores on lateral pigment line, opercle, and at pectoral fin base.

Postlarval Development

Stages 33 and 34: assimilation of yolk, day 12, 311 hours, 10.0 mm. Yolk assimilated, proctodeum open to form anus. Opercles cover two anteriormost gills. Otoliths present in auditory vesicles. Pectoral fins with 3 rays; caudal fin with 3 or 4 rays; no trace of dorsal or anal fins. Spleen forming posterior to liver. Posterior end of notochord (urostyle) upcurved. Pigmentation increased on all aspects except lateral pigment line; melanophores appearing on gas bladder.

Stage 35: early postlarva, day 17, 430 hours, 12.0 mm. Caudal fin-rays increased to 7 to 9. Opercles cover gills. Median fin fold thickened and expanded at sites of anal and dorsal fins. Food materials in stomach; feces passing through intestine. All pigmentation excepting lateral pigment line intensified.

Stage 36: dorsal and anal fin-ray rudiments, day 40, 960 hours, 15.5 mm (Fig. 7). Fin-ray rudiments in dorsal and anal fins; caudal fin with full complement of ossified rays. Gas bladder constricting into two chambers. Melanophores appearing on posterior part of lateral pigment line.

Stage 37: middle postlarva, day 48, 1152 hours, 20.0 mm. Rays of dorsal and anal fins partially ossified; pelvic fins rudimentary as gatherings of mesenchyme; caudal fin becoming emarginate. Gas bladder two chambered. Urogenital papilla apparent. Mouth terminal;

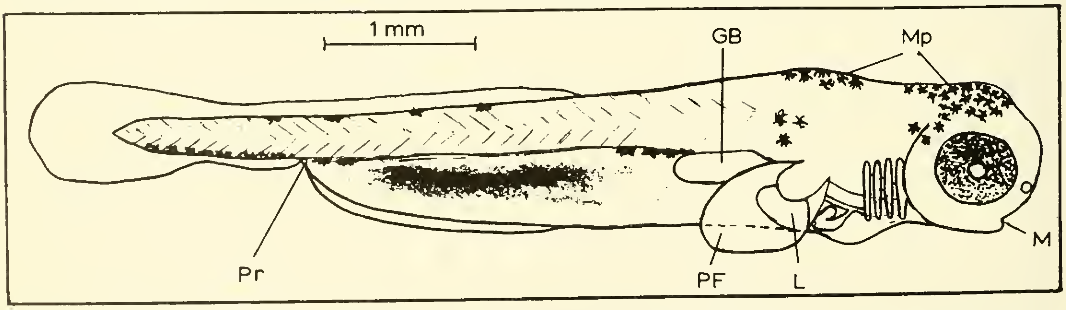


Fig. 6. Late prolarva of razorback sucker, *Xyrauchen texanus*; legend as in Figures 1 to 5 when applicable, and GB = gas bladder, L = liver, M = mouth, Mp = melanophores, and PF = pectoral fin.

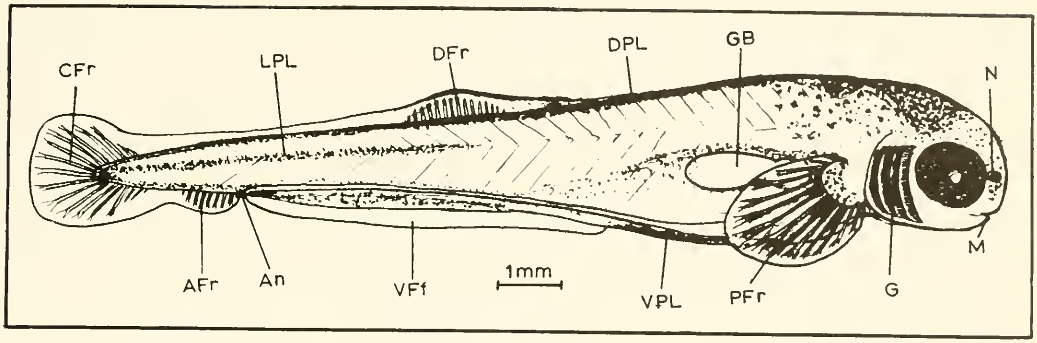


Fig. 7. Postlarva of razorback sucker, *Xyrauchen texanus*, at beginning of fin-ray development; legend as in Figures 1 to 6 when applicable, and AFr = anal fin-rays, An = anus, CFr = caudal fin-rays, DFr = dorsal fin-rays, DPL = dorsal pigment line, G = gills, LPL = lateral pigment line, N = naris, PFr = pectoral fin-rays, and VPL = ventral pigment line.

lips formed, small papillae on both upper and lower lips. Melanophores increasing over body; ossified fin rays and gills acquiring pigment; larvae dark dorsally and lighter ventrally and in eye region.

Stage 38: pelvic fin rudiments, day 50, 1200 hours, 20.8 mm. Pelvic fin rudiments in form of small crescentic folds.

Stage 39: pelvic fin buds, day 54, 1296 hours, 23.5 mm. Pelvic fin buds in form of thin membranous paddles, not movable.

Stage 40: pelvic fin rudiments, day 64, 1536 hours, 27.0 mm. Six pelvic fin-ray rudiments within pelvic fin membranes; fin movable. Dorsal and anal fin-rays completely ossified. Mouth beginning to shift ventrally, papillae highly developed on lips.

Stage 41: ossification of pelvic fin-rays, day 70, 1680 hours, 32 mm. Rays partially ossified in pelvic fins; median fin membrane persisting ventrally and anterior to pelvic fins greatly reduced; dorsal and anal fins separated from caudal fin.

Stage 42: late postlarva, day 75, 1800 hours, 35 mm (Fig. 8). Pelvic fin-rays ossified. Median fin membrane persisting only between anus and pelvic fins. Full complements of fin-rays in all fins: dorsal, 15-16; caudal, 19; anal, 8; pelvic, 9-9; and pectoral, 13-15–13-15. Narial flap formed. Alimentary tract looped once to left just posterior to stomach, mouth ventral. Acoustico-lateralis system formed on anterior half of body.

Juvenile Development

Stage 43: scale rudiments, day 105, 2520 hours, 43.0 mm. Scale rudiments present on ventro-lateral surfaces; median fin membrane eliminated.

Stage 44: scales, day 125, 3000 hours, 45.0 mm. Scales distinctly visible except medially on dorsum and ventrum.

Stage 45: nuchal keel, day 227, 5448 hours, 90.0 mm (Fig. 9). Scalation completed. Acoustico-lateralis system completed. Nuchal

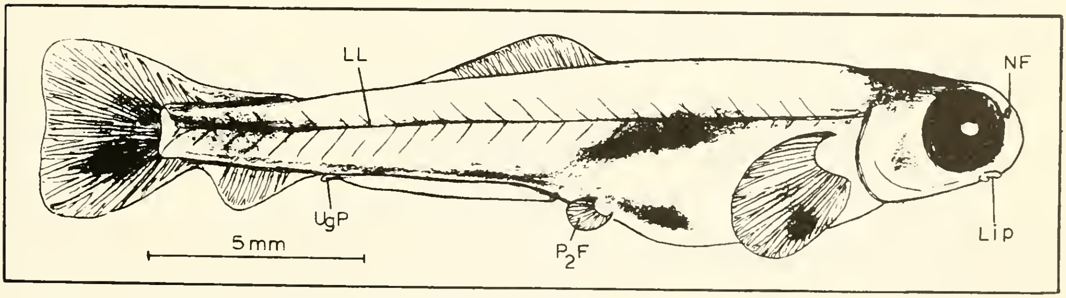


Fig. 8. Late postlarva of razorback sucker, *Xyrauchen texanus*; legend: LL = lateral line, Lip = papillose lips, NF = nasal flap, P_2F = pelvic fin, and UgP = urogenital papillus.

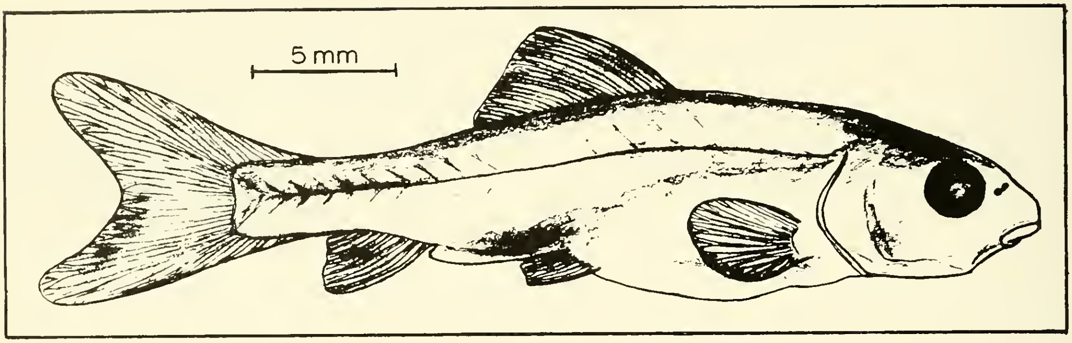


Fig. 9. Juvenile of razorback sucker, *Xyrauchen texanus*, shortly after initiation of nuchal keel.

keel evident to touch on predorsum. Except for further development of nuchal keel, evident to the eye at a 250–300 days of age (Fig. 10), morphogenesis is completed. Individuals from the 1974 cohort achieved sexual maturity in their sixth year of life (Minckley 1983).

SUMMARY

Fertilized, water-hardened ova of *Xyrauchen texanus* were 1.8 mm in diameter from females hormone-induced to mature and 2.9 mm from females that matured naturally.

Eggs were adhesive for 3 to 4 hours after fertilization. Cleavage was completed in 24 hours at temperatures varying from 13 to 17 C; further development was at 20 C. Gastrulation occurred at 34 hours. The notocord separated from the mesoderm at 47 hours, and eye rudiments and brain cavities were distinguishable at 49 hours. The tail process formed at 57 hours (2.5 mm). Heart beat began at 83 hours, and blood circulation was established at 117 hours. Embryos began violent flexing and some ruptured their chorions at that time. All hatched between 125 and 131 hours after fertilization.

Embryos were 6.8 to 7.3 mm TL at hatching. The yolk sac is tubular, and the head flexes over it at a 45 degree angle to the body axis. The pectoral fin buds, noted at 120 hours (6.8 mm), became paddlelike at 162 hours (8.0 mm), and first were movable at 238 hours (9.0 mm). The continuous, median fin fold first noted on caudal and posterodorsal areas at 103 hours (5.3 mm), began to develop on the venter (behind the proctodeum) at 142 hours (7.5 mm), and was continuous at 162 hours (8.0 mm). The opercles began forming at 162 hours (8.0 mm). The gas bladder first appeared at 238 hours (9.0 mm). The lower jaw became movable and prolarvae began directed swimming to the sur face to feed at that time; eye pigment complete and black. Melanophores developed over mid- and hindbrain and on paired dorsal, paired dorso-visceral, and unpaired midventral pigment lines between 162 and 238 hours (8.0 and 9.0 mm). There was no lateral

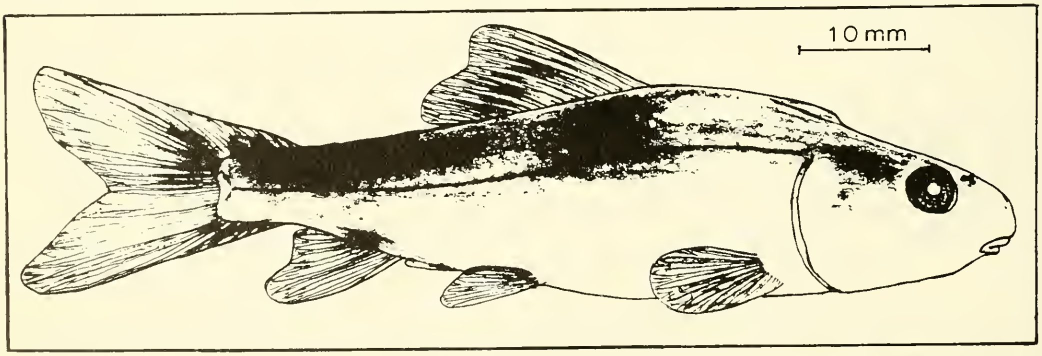


Fig. 10. Juvenile of razorback sucker, *Xyrauchen texanus*, with essentially adult morphology.

pigmentation at 9.0 mm. Melanophores on the dorsum are large and stellate, as also recorded by Winn and Miller (1952). At 263 hours (9.0+ mm) fin rays were not yet visible in any fin.

Yolk was completely assimilated at 311 hours (10.0 mm) and the proctodeum opened to form the anus. The urostyle became upturned between 263 and 311 hours, and 3 to 4, ventral, caudal fin-rays formed by the last time period. Pectoral fins had developed three rays, but there were no rays in the dorsal and anal fins. Median fin folds were thickened and expanded at the sites of the future dorsal and anal fins at 430 hours (12.0+ mm), and the opercles fully covered the gills. Dorsal and anal fin-ray rudiments, and a lateral pigment line appeared at 960 hours (15.5 mm). The gas bladder had by this time constricted toward the two-chambered condition. Pelvic fins appear as swellings of mesenchyme and the caudal fin becomes emarginate at 1152 hours (20.0 mm). The pelvic fin buds were nonmovable, membraneous paddles at 1296 hours (23.5 mm); movement and pelvic fin-rays had appeared at 1536 hours (27.0 mm).

Scale rudiments were first noted at 2520 hours (43.0 mm) on ventrolateral body surfaces. By 3000 hours, lepidogenesis was complete on all but the median areas of the dorsum and ventrum. The nuchal keel appeared about 5000 hours after fertilization.

ACKNOWLEDGMENTS

This research was supported, in part, by U.S. Fish and Wildlife Service Contract 14-16-0002-3585 to Arizona State University. We thank personnel at Willow Beach National Fish Hatchery for assistance in obtaining and rearing young of razorback suckers. Permits for collection of wild fish were granted by Arizona Game and Fish Department. J. P. Collins and R. W. McGaughey read and commented on the manuscript.

LITERATURE CITED

BALINSKY, B. I. 1948. On the development of specific characters in cyprinid fishes. Proc. Zool. Soc. London 118:335–344.

DOUGLAS, P. A. 1952. Notes on the spawning of the razorback sucker, *Xyrauchen texanus* (Abbott). California Fish and Game 38(2):149–155.

FUIMAN, L. A., AND D. C. WITMAN. 1979. Descriptions of catostomid fish larvae: *Catostomus catostomus* and *Moxostoma erythrurum*. Trans. Amer. Fish Soc. 108(6):604–619.

FUIMAN, L. A., AND J. R. TROJNAR. 1980. Factors affecting egg diameter of white sucker (*Catostomus commersoni*). Copeia 1980(4):699–704.

LONG, W. L., AND W. W. BALLARD. 1976. Normal embryonic stages of the white sucker, *Catostomus commersoni*. Copeia 1976(2):342–351.

MINCKLEY, W. L. 1983. Status of the razorback sucker, *Xyrauchen texanus*, in the lower Colorado River basin. Southwest. Nat. 28(2): In press.

PISTER, E. P. 1981. The conservation of desert fishes. Pages 411–446 *in* R. J. Naiman and D. L. Soltz, eds., Fishes in North American deserts. John Wiley and Sons, New York.

RYDER, J. A. 1885. On the development of viviparous osseous fishes. Proc. U.S. Nat. Mus. 85:128–162.

STEWART, N. H. 1926. Development, growth and food habit of the white sucker, *Catostomus commersonii* LeSueur. Bull. U.S. Bur. Fish. 42:147–183.

TAVOLGA, W. N. 1949. Embryonic development of the platyfish (*Platypoecilus*), the swordtail (*Xiphophorus*), and their hybrids. Bull. Amer. Mus. Nat. Hist. 94(4):161–230.

TONEY, D. P. 1974. Observations on the propagation and rearing of two endangered fish species in a hatchery environment. Proc. Ann. Conf. West. Assn. State Game Fish Comm. 54:252–259.

WINN, H. E., AND R. R. MILLER. 1954. Native postlarval fishes of the lower Colorado River basin, with a key to their identification. California Fish and Game 40(3):273–285.

BEHAVIOR AND HABITAT PREFERENCES OF RING-NECKED PHEASANTS DURING LATE WINTER IN CENTRAL UTAH

Jeffrey G. Skousen[1] and Jack D. Brotherson[1]

Abstract.— Ring-necked pheasant behavior and habitat preferences were studied during late February along benches of the Wasatch Mountains in central Utah. Seven behavioral categories were used to classify pheasant activities during three time periods of the day. Eating, alert, and movement behavior were the most frequent activities during all periods of the day. Significant differences ($p < .01$) were found between morning and midday behavior and between midday and evening behavior. Pheasants fed in open areas during morning hours then retreated into heavy cover during midday periods. The birds remained in heavy cover until late afternoon. Pheasants then moved away from heavy cover into semiopen areas to feed as evening approached.

The ring-necked pheasant (*Phasianus colchicus*) is a native of eastern Asia. Its first successful importation into the United States was in Oregon in 1881 (Allen 1956). Later, in 1888, the birds were also successfully transplanted into the eastern part of the United States (Rue 1980). Pheasants were introduced into the state of Utah about 1890 (Rawley and Bailey 1972). Distribution of pheasants in Utah has increased so that nearly all suitable habitat is occupied. This habitat is primarily within the irrigated farmlands of the state, which comprises about 2 to 4 percent of the total land area (Olsen 1977). The pheasant population of Utah reached a peak in the 1950s and has steadily decreased. This downward trend has been a result of habitat deterioration (Nish 1973).

Pheasant distribution is primarily affected by the habitat, soil, and climate of an area. Christensen (1951) found that together soils and climate determined whether or not pheasants occurred in an area of Missouri. Dale (1956) has suggested that a combination of high temperature and high humidity have probably inhibited the spread of pheasants into the southeastern United States. Soils and climate restrict pheasant distribution because climate controls soil development and food quality. Climate is especially important during the nesting season because hens leave their eggs for a period of time after laying, thus exposing them to climatic conditions (Graham and Hesterberg 1948). Pheasant eggs generally show reduced hatchability as temperatures increase (Yeatter 1950). Wood and Brotherson (1982) found that nesting sites were specifically dependent upon total living ground cover and high amounts of cover surrounding the nesting cavity.

Soils seem to influence pheasant distribution through their effects on vegetation. In the United States much of the fertile soil is cultivated with corn and other grains, which have been shown to be preferred pheasant food (Leedy and Hicks 1945). Christensen (1951) reported that the distribution of pheasants in Missouri coordinated with highly fertile soils used for agriculture. Edminster (1954) agreed that pheasants preferred agricultural land that produced grain. Pheasants showed similar distribution patterns in Wisconsin (Hine 1964), Ohio (Leedy and Hicks 1945), and Illinois (Kimball et al. 1956). In Montana and Utah, conversion of grain-producing acreage to hayfields has resulted in a decline of pheasant densities (Weigand 1973, Nish 1973). Winter cover and nesting habitat are the two major deficiencies in pheasant habitat in the Great Lake States (MacMullan 1961, McCabe et al. 1956), the Dakotas (Kimball et al. 1956), the northwest (Lauckhart and McKean 1956), New York (Perry 1946), and California (Hart et al. 1956). In areas of Utah where adequate cover is lacking, winter kill of pheasants has been shown to be high (Yeager et al. 1956). Wood and Brotherson (1981) found that in most areas of Utah overwinter pheasant mortality was not due to winter weather.

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Pheasants are omnivorous; eating waste grains, weed seeds, green vegetation, and numerous insects (Rue 1980, Olsen 1977, Rawley and Bailey 1972). Different proportions of these foods are eaten depending on area, location (Cottam 1929, Swenk 1930, Gigstead 1937, Fried 1940, Trautman 1952, Korschgen 1964), and the age of the bird (Rue 1980, Edminster 1954). In Utah, adult pheasant diets are comprised mostly of grain (36.7 percent) and vegetation (20.4 percent) (Cottam 1929). In the midwest, 70 to 85 percent of the total diet of adult pheasants is cultivated grains (Dalke 1937, Trautman 1952, Korschgen 1964, Fried 1940, Gigstead 1937, Swenk 1930). Juvenile birds, for the first three weeks, eat insects (Rue 1980, Edminster 1954, Dalke 1937, Loughrey and Stinson 1955) then switch to vegetation after that. Few studies have been done on actual daily behavioral patterns of the ring-necked pheasant. Burger (1966) studied aggressive territorial behavior of male ring-necked pheasants during the mating season. Kuck et al. (1970) reported on the renesting behavior of hen pheasants in South Dakota. This paper is concerned with habitat preferences and daily behavior patterns of pheasants in central Utah during late February.

Study Area

The study area (40 ha) is located on a bench of the Wasatch Mountains near Provo, Utah. Thirty percent of the area is a shrub study plot used by the Intermountain Forest and Range Experiment Station, 20 percent is a mature apricot orchard (used for pasture) and 50 percent is native rangeland. The area has a western aspect with loamy cumulic calcixeroll soils. Slopes are generally 3 to 10 percent and elevation is approximately 1400 m (4600 ft). A housing tract is located on the lower edge of the study area, and one paved and heavily used road runs through the center of the area.

Methods

Five days of 4 to 8 hours each were spent observing pheasants during 20–24 February 1982. Days during which the study took place were generally clear and sunny with some scattered clouds. Approximately 15 to 25 cm (6–10 in) of snow was on the ground when the study was initiated but melted before completion. Temperatures on these days ranged from 35 F in the morning hours to 60 F during afternoons. Observations were made with the aid of binoculars and a 20 power spotting scope. One individual was chosen (a male normally) and observed closely. At one-minute intervals, the individual was classified as to his behavior at that moment. The behavior classes considered were: eating, resting, grooming, aggressive, alert, movement, and comfort behavior (Table 1). In between the minute evaluations, interaction between the selected individual and others, as well as other activities that influenced the group, were recorded. Habitat utilized by the birds was also noted and later classified into habitat types.

Results and Discussion

Pheasant behavior was variable during the day but was very similar during morning and

Table 1. Activities associated with each behavior category.

Category	Behavior
Eating	Head is down, pecking material on the ground.
Resting	Eyes closed and relaxed.
Grooming	Fluffing feathers.
Aggressive	Cause another bird to move or pecking other birds.
Alert	Watching, alert, and ready to fly. Looking at something moving or making noises close by.
Movement	Walking, running, or flying.
Comfort	Looking without being alert and not at anything in particular. Scratching.

Table 2. Behavioral classes and percent of time spent in each class during three time periods.

Behavioral class	Morning 6:00–10:00 (percent)	Midday 10:00–4:00 (percent)	Evening 4:00–8:00 (percent)
Eating	47.5	7.0	51.5
Resting	0.0	1.0	0.0
Grooming	3.5	4.0	0.5
Aggressive	2.5	2.0	0.5
Alert	31.5	50.0	22.0
Movement	14.5	32.0	20.5
Comfort	0.5	4.0	6.5

evening hours (Table 2). Approximately 50 percent of the time spent during these periods was in eating, and another 40 to 45 percent of the time was divided between alert (25 percent) and/or movement (20 percent) behavior (Table 2). Grooming, aggressive, and comfort behavior contributed the balance of the time spent (6–7 percent). However, during midday periods, most of the time was spent in being alert (50 percent) and/or moving (32 percent) (Table 2). Eating behavior during this period was reduced to 7 percent. Evening behavior of pheasants, though similar to morning periods, seemed to be less affected by noises made by man. There was a highly significant difference ($p<.01$) in the amount of time spent in each behavior category across a day. Chi-square tests showed no significant difference in behavior patterns between morning and evening periods of the day. However, significant differences ($p<.01$) were observed between morning and midday behavior and between midday and evening behavior ($p<.01$). Eating, alert, and movement behavior were the most frequent activities during all times of the day. Spearman's rank correlation (Snedecor and Cochran 1968) showed no significant differences between rankings of observed behavior during morning, midday, and evening.

Habitats utilized by the pheasants were classified into 5 types. Table 3 shows these habitat types and their major associated plant species. Habitat preference varied between periods of the day (Table 4). During morning hours, pheasants were observed to be in areas that offered little cover and where pasture grasses were available (Tables 3, 4). Numerous insects were observed in the grass pasture. The birds may have been eating the insects rather than the vegetation. They moved to areas of heavier cover (ditch banks and fence rows) as activities of man increased and as disturbances from other animals increased. During midday periods, all pheasants observed were found in fence rows or ditch

TABLE 3. Species list in each habitat type.

Species	Orchard grass apricot pasture	Orchard grass apricot pasture fence row	Wooded fence row	Ditch banks	Forest Service plots
Agoseris glauca	x	x	x		
Agropyron repens	x			x	
Agropyron spicatum	x	x	x	x	x
Ambrosia psilostachya	x	x	x	x	x
Artemisia tridentata					x
Bromus tectorum	x	x	x	x	x
Ailanthus altissima			x		
Chrysothamnus nauseosus					x
Cirsium arvense	x	x			
Cirsium vulgare	x	x			
Descurainia sophia	x	x		x	x
Dactylis glomerata	x	x	x	x	
Erodium cicutarium			x	x	x
Grindelia squarrosa				x	x
Kochia prostrata					x
Kochia scoparia	x	x		x	x
Linaria vulgaris					x
Penstemon spp.					x
Petradoria pumila				x	x
Poa secunda	x	x	x	x	x
Prunus armenica	x	x			
Populus angustifolia			x		
Populus fremontii			x	x	
Rosa woodsii		x	x		
Robinia pseudoacacia			x		
Salix fragilis			x		
Salsola kali				x	
Syringa vulgaris			x		
Ulmus pumila		x			
Xanthium spp.	x	x			

TABLE 4. Habitat and cover preferences and percent of time spent in each habitat.

Habitat type	Morning (percent)	Midday (percent)	Evening (percent)
Orchard grass apricot pasture	29	17	0
Orchard grass apricot pasture fence row	62	0	0
Wooded fence rows	0	21	0
Ditch banks	9	62	54
Forest Service plots	0	0	46

banks (Table 4). Evening hours were spent along ditch banks and shrub plots that offered some cover but which were generally more open than the areas frequented at midday.

Movement from open areas in the morning to areas of heavier cover (i.e., ditch banks and fence rows) depended on the amount and kind of disturbances in the immediate area. Cars starting and children walking to and from school generally caused the pheasants to move slowly into heavier cover. Pheasants ran and flew as crows passed overhead. Middays were spent in heavy cover and the birds did not move unless flushed. Evenings were generally spent feeding and moving away from heavy cover while being very cautious and aware of the activities around them.

LITERATURE CITED

ALLEN, D. L., ed. 1956. Pheasants of North America. Stackpole Co., Harrisburg, Pennsylvania, and Wildlife Management Institute, Washington, D.C.

BURGER, G. V. 1966. Observations on aggressive behavior of male ring-necked pheasants in Wisconsin. J. Wildl. Manage. 30(1):57–64.

COTTAM, C. 1929. The status of the ring-necked pheasant in Utah. Condor 31(3):117–123.

CHRISTENSEN, D. M. 1951. History and status of the ring-necked pheasant in Missouri. Missouri Cons. Commission.

DALE, F. H. 1956. Pheasants and pheasant populations. Pages 1–42 *in* Allen 1956.

DALKE, P. L. 1937. Food habits of adult pheasants. Pages 139–142 *in* McAtee 1945.

EDMINSTER, F. C. 1954. American game birds of fields and forest. Charles Scribner's Sons, New York.

FRIED, L. A. 1940. The food habits of the ring-necked pheasant in Minnesota. J. Wildl. Manage. 4(1):27–36.

GIGSTEAD, G. 1937. Habits of Wisconsin pheasants. Wilson Bull. 49(1):28–34.

GRAHAM, S. A., AND G. HESTERBERG. 1948. The influence of climate on the ring-necked pheasant. J. Wildl. Manage. 12(1):9–14.

HART, C. M., B. GLADING, AND H. T. HARPER. 1956. The pheasant in California. Pages 90–158 *in* Allen 1956.

HINE, R. L. 1964. Status of farm game in Wisconsin. A Report of the Farm Game Working Group of the Natural Resources Committee of State Agencies Land Subcommittee. Madison, Wisconsin.

KIMBALL, J. W., E. L. KOZICKY, AND B. A. NELSON. 1956. Pheasants of the plains and prairies. Pages 204–263 *in* Allen 1956.

KORSCHGEN, L. J. 1964. Foods and nutrition of Missouri and Midwestern pheasants. Trans. N. Am. Wildl. Conf. 29:159–181.

KUCK, T. L., R. B. DAHLGREN, AND D. R. PROGULSKE. 1970. Movements and behavior of hen pheasants during the nesting season. J. Wildl. Manage. 34(3):626–630.

LAUCKHART, J. B., AND J. W. MCKEAN. 1956. Chinese pheasants in the Northwest. Pages 43–89 *in* Allen 1956.

LEEDY, D. L., AND L. E. HICKS. 1945. The pheasants of Ohio. Pages 57–130 in McAtee 1945.

LOUGHREY, A. G., AND R. H. STINSON. 1955. Feeding habits of juvenile ring-necked pheasants on Pelee Island, Ontario. Canadian Field Nat. 69(2):59–65.

MACMULLAN, R. A. 1961. Ring-necked pheasant habitat management in the United States. Trans. N. Am. Wildl. and Nat. Resour. Conf. 26:268–272.

MCCABE, R. A., R. A. MACMULLAN, AND E. H. DUSTMAN. 1956. Ringneck pheasants in the Great Lakes region. Pages 264–356 *in* Allen 1956.

NISH, D. H. 1973. Pheasant habitat trends in Utah—can they be reversed? Proc. Pheasant Habitat Symposium, Salt Lake City, Utah. 11 July 1973.

OLSEN, D. W. 1977. A literature review of pheasant habitat requirements and improvement methods. Utah Div. of Wildl. Res. Pub. No. 77-7. 144 pp.

PERRY, R. F. 1946. An appraisal of pheasant abundance in New York State during 1945 and some of the factors responsible for the recent decline. Trans. N. Am. Wildl. Conf. 11:141–155.

RAWLEY, E. V., AND W. J. BAILEY. 1972. Utah upland game birds. Utah Div. of Wildl. Res. Pub. No. 63-12. 31 pp.

RUE, L. L. 1980. Wildlife profiles: ringneck pheasant. American Hunter Vol. 8, No. 3, March 1980, pp. 40–43.

SNEDECOR, G. W., AND W. G. COCHRAN. 1968. Statistical Methods. 6th ed. Iowa State Univ. Press, Ames, Iowa. 593 pp.

SWENK, M. H. 1930. The food habits of the ring-necked pheasant in central Nebraska. Nebraska Agric. Expt. Sta., Research Bull. 50. 33 pp.

TRAUTMAN, C. G. 1952. Pheasant food habits in South Dakota. Tech. Bull. No. 1, South Dakota Dept. Game, Fish and Parks.

WEIGAND, J. P. 1973. Pheasant population and habitat trends in Montana. Proc. Pheasant Habitat Symposium, Salt Lake City, Utah. 11 July 1973.

WOOD, A. K., AND J. D. BROTHERSON. 1981. Overwinter survival of ring-necked pheasants in Utah. Great Basin Nat. 41(2):247–250.

_____. 1982. Microhabitat and nest site selection by ring-necked pheasants. Great Basin Nat. 41:457–460.

YEAGER, L. E., J. B. LOW, AND H. J. FIGGE. 1956. Pheasants in the arid Southwest. Pages 159–203 *in* Allen 1956.

YEATTER, R. E. 1950. Effects of different preincubation temperatures on the hatchability of pheasant eggs. Science 112(2914):529–530.

RHYTHM OF FECAL PRODUCTION AND PROTEIN CONTENT FOR BLACK-TAILED JACKRABBITS

William D. Steigers, Jr.[1], Jerran T. Flinders[1], and Susan M. White[1,2]

Abstract.— The cyclical phenomenon of soft and hard formation of feces in desert black-tailed jackrabbits (*Lepus californicus deserticola*, Mearns) was investigated. Sixty-nine blacktails were shot between 0525 hours and 1508 hours over a 4-day period. The average age was 314 days for all black-tails. The large intestine was removed and linear measurements taken. Overall length of the large intestine averaged 163.3 cm; mean length of the colon was 51.5 cm and average length of the rectum was 111.8 cm. Moisture content for soft and hard pellets averaged 79.5 percent and 74.1 percent, respectively. Protein content of soft and hard pellets averaged 45.8 percent and 14.3 percent, respectively. The black-tails began the transition from hard to soft pellets as early as 0414 hours, and nearly all had completed the reverse transition by 1508 hours. Female black-tails began both early morning and afternoon transitions significantly later than the males. Reasons for the apparent sexual partitioning are proposed.

It has long been known that the domestic rabbit produces both hard and soft fecal pellets (Morot 1882). The hard pellets are the normal waste product of the digestive tract and are the type of feces found in the field. The soft "pellets" are a special product of the cecum, and are reingested directly from the anus and swallowed whole. The position assumed by the black-tailed jack rabbit when reingesting soft pellets is described by Lechleitner (1957).

The method whereby a rabbit can pass two kinds of feces, soft and hard pellets, has been conjectured by Eden (1940) and Thacker and Brandt (1955). The latter suggest hard fecal pellets are formed by material that has passed through the base of the cecum without being mixed with the main content of the cecum. The soft feces are formed by emptying the major portion of the cecum, in a cyclic manner, by a strong contraction of the spiral muscle (Thacker and Brandt 1955). The composition of the soft feces is comparable to that of the cecal contents in protein, crude fiber, and other proximate nutrients (Eden 1940, Olsen and Madsen 1944). Cecectomized rabbits do not excrete typical soft feces (Herndon and Hove 1955). Although the hard pellets exit the body as firm, nearly spherical excreta, the soft feces are generally excreted as clusters of soft, moist, pellets with a distinctive sheen. Soft feces usually are higher in protein than hard feces (Herndon and Hove 1955). Soft pellets consist largely of bacteria surrounded by a proteinaceous membrane deposited posterior to the colon (Griffiths and Davies 1963).

Several authors have reported the cycle or rhythm of production of hard and soft pellets in rabbits. Although Southern (1942) reported the frequency of coprophagy (or cecaphagy) in the wild rabbit as twice daily, most authors suggest a single such daily period (Meyer 1955, Watson and Taylor 1955, Lechleitner 1957). Spencer (1955) studied rhythms of reingestion in white-tailed jackrabbits (*Lepus townsendii*), snowshoe hares (*L. americanus*), and New England cottontails (*Sylvilagus transitionalis*). Hansen and Flinders (1969) suggested that reingestion in white-tailed jackrabbits, black-tailed jackrabbits, snowshoe hares, and European hares takes place in the late morning hours. Thacker and Brandt (1955) found that the excretion of hard and soft feces by domestic Dutch rabbits was a consistent daily phenomenon both as to time and quantity. Lechleitner (1957) reported the percent of soft feces in the recta of 160 black-tailed jackrabbits killed periodically throughout every month of the year. Although the exact time of death was not known, it had been approximated for the 160 black-tails. However, no known study reported to date has attempted to quantify the exact periodicity of soft and hard feces formation in wild populations of black-tailed jackrabbits.

---

[1] Wildlife and Range Resources Graduate Program, 401 WIDB, Brigham Young University, Provo, Utah 84602.

[2] Present address: Native Plants, 400 Wakara Way, Salt Lake City, Utah 84108.

The purpose of this study was to quantify the exact time periods of production as well as transition periods for hard and soft feces in wild populations of black-tailed jackrabbits in north central Utah.

STUDY AREA

This study was conducted in two areas in north central Utah. Rabbits were sampled from rangelands near Fountain Green, Sanpete County, Utah, and from the U.S. Forest Service Benmore Experimental Area near Vernon, Tooele County, Utah. The elevation of the study areas are approximately 1830 m and 1770 m, respectively. Each receives about 35 cm of average annual precipitation, with most of this in the form of snow from October through May.

The woody vegetation of both areas is dominated by rubber rabbitbrush (*Chrysothamnus nauseosus*) and big sagebrush (*Artemisia tridentata*). Prominent grasses include bluebunch wheatgrass (*Agropyron spicatum*), fairway wheatgrass (*A. cristatum*), and Sandberg bluegrass (*Poa sandbergii*).

METHODS

Desert black-tailed jackrabbits were collected with shotguns on four days during March 1980. Predawn collections were conducted with the aid of a spotlight. The first 59 black-tails were collected from the Fountain Green study area: 8 black-tails on 8 March, 19 blacktails on 15 March, and 32 blacktails on 18 March. An additional 10 black-tails were taken 22 March from the Benmore study area.

All black-tails were taken opportunistically, and the exact time of death to the nearest minute was recorded for each hare shot. An attempt was made to sample black-tails during all time periods between initiation of the hard-to-soft pellet transition in early morning to the soft-to-hard pellet transition in the early afternoon. Entrails of the black-tails were removed within 3 hours after being shot, and frozen.

The left eyeball was removed for age determination using the eye lens-weight method and age curve described by Tiemeier (1965). The eyeball was held in 10 percent buffered formalin for one week. The lens was then removed from the eyeball and placed in an oven at 90 C. The lens was considered dry after 48 or more hours, when repeated weighings to 0.001 g resulted in no additional weight loss.

In the laboratory, the portion of the intestinal tract from the anus to the juncture of the small intestine and ileocecal valve were separated by severing the mesentery. The overall length of the large intestine from the ileocecal valve to the anus was measured, as well as the length from the ileocecal valve to the taenia coli muscle. Fecal samples of both hard and soft pellets were taken, if present, from the rectum (between taenia coli muscle and anus). Hard pellets could not be accurately separated from soft pellets in the large intestine until the feces passed the taenia coli muscle. If a transitory condition between hard and soft pellets was noted, the length of the rectum between the transition and taenia coli muscle was measured. The precise time the transition occurred at the taenia coli muscle was calculated by backdating the transition for a 45 cm per hour rate of passage. Fecal samples were immediately weighed to 0.001 g, and then placed in a drying oven at 83 C for 24 hours to determine moisture content.

Within approximately one month, the fecal samples were again oven dried, cooled in a dessicator, ground, and analyzed for nitrogen content using the macro-Kjeldahl technique (Black et al. 1965). Samples of feces <1 g were pooled with fecal samples from black-tails of the same sex that were collected at approximately the same time.

RESULTS AND DISCUSSION

Measurements

The 69 (33 males, 36 females) black-tailed jackrabbits were collected between 0525 hours and 1508 hours. The average age for all black-tails was 314 ± 141 days (SD) ($N = 67$, range 153–746 days). The average age for males was 315 ± 142 days ($N = 31$, range

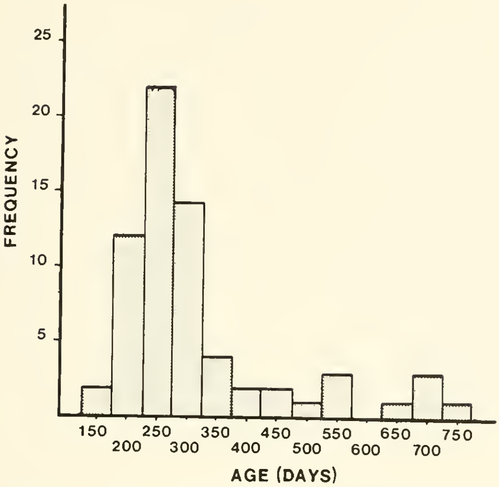


Fig. 1. Histogram illustrating age distribution in days of black-tailed jackrabbits collected for analysis.

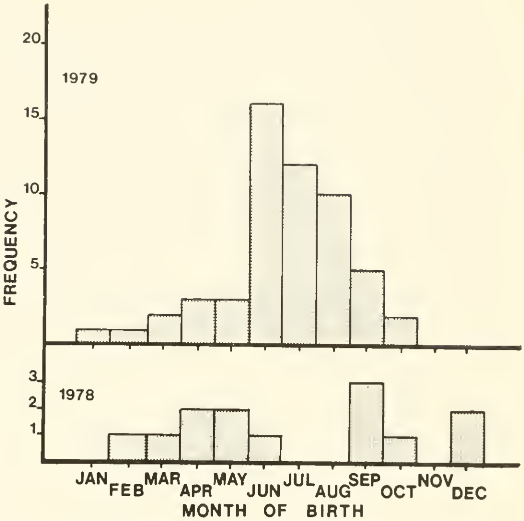


Fig. 2. Distribution of months of birth for black-tailed jackrabbits collected for analysis that were born during 1978 and 1979.

153–718 days) and for females was 313 ± 143 days ($N = 36$, range 169–746 days). The average age by 50-day intervals for black-tails in our sample is illustrated in Figure 1. Black-tails born during 1979 comprised 84 percent of the sample; all remaining black-tails were born during 1978. Seventy-two percent of all black-tails collected were between 175 and 325 days of age and were born during the period June through September. A breakdown by year and month for black-tails born in 1978 and 1979 is represented in Figure 2.

The average overall length of the large intestine was 163.2 ± 17.2 cm ($N = 66$, range 134–212 cm). The mean length of the colon was 51.5 ± 5.0 cm ($N = 66$, range 43–72 cm) and of the rectum was 111.7 ± 14.6 cm ($N = 66$, range 85–143 cm). Correlation between the measurements of overall length of the large intestine ($r = 0.31$, $P < 0.05$), colon length ($r = 0.25$, $P < 0.05$), and rectal length ($r = 0.29$, $P < 0.05$) with age of the black-tail was relatively low. However, correlation between the overall length of the large intestine and colon length ($r = 0.62$, $P < 0.001$) and the overall length of the large intestine and rectum length ($r = 0.96$, $P < 0.001$) was much higher. The correlation between colon length and rectal length was $r = 0.38$ ($P < 0.005$).

Average percent moisture of soft pellets from 58 samples collected from the rectum was 79.5 ± 1.8 percent (range 74.2–83.0 percent). Average percent moisture of hard pellets from 20 samples collected from the rectum was 74.1 ± 2.8 percent (range 67.8–78.8 percent). The average moisture content for soft pellets was significantly greater ($P < 0.001$) than that of hard pellets using an unpaired T-test. This comparison included 12 samples where hard and soft pellets were removed from the same rectum. This indicates a significant change in moisture content associated with the rapid change in the type of pellet produced at the taenia coli muscle.

Protein

Protein content (percent N × 6.25) of soft and hard pellets averaged 45.8 ± 5.9 percent ($N = 8$, range 35.0–51.5 percent) and 14.3 ± 5.6 percent ($N = 9$, range 7.1–23.3 percent), respectively. Derived protein values compare favorably with those reported by other authors. Herndon and Hove (1955) reported 41.9 percent protein for soft pellets and 14.8 percent protein for hard pellets in experimental California-white rabbits (*Oryctolagus cuniculus*). Griffiths and Davies (1963) estimated soft feces of rabbits contained 24.4 percent protein, 81 percent of which was in the form of bacterial cells. They reported bacterial cells composed 56 percent of the dry weight of soft feces. Other comparative estimates of protein content in the soft feces of domestic rabbits were 37.8 percent (Huang et al. 1954) and 28.5 percent

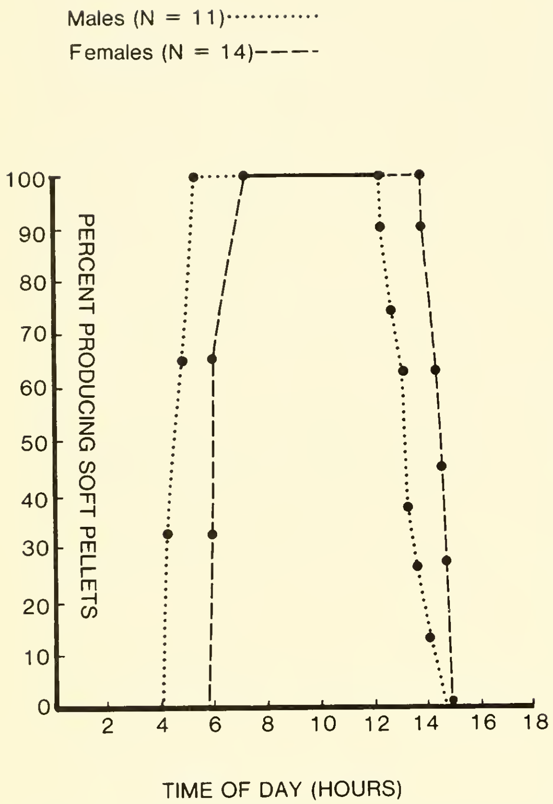


Fig. 3. Percent of male and female black-tailed jackrabbits producing soft pellets at the taenia coli muscle in the large intestine.

for soft feces and 9.2 percent for hard feces (Kulwich et al. 1953). Thacker and Brandt (1955) reported 37.4 ± 3.2 percent protein for soft feces and 18.7 ± 1.7 percent protein for hard feces in the Dutch rabbit.

Pellet Transition Periods

When a transition zone was found in the rectum of a black-tail, the degree of distinctness between the two types of pellets was noted. In our samples, 17 of 19 transition zones were very well defined and distinct, often with immediately adjacent pellets of the two types. In the other two cases, the transition zone included up to 10 cm of semihard pellets separating the hard and soft pellet types. Distinct transition zones were found for both early morning and afternoon periods of pellet transition.

Male black-tailed jackrabbits had initiated the transition from hard to soft pellets as early as 0414 hours (Fig. 3). The transition period for both sexes ranged from 0414 to approximate completion by 0715 hours. Males sampled were complete in the initiation of their transition by 0500 hours, whereas females sampled were not all complete by 0700 hours (Fig. 3). All black-tails had made the transition to the production of soft pellets by 0730 hours. Soft pellets made up the entire composition of the rectum in all black-tails by 0915 hours.

Several male black-tails began the transition from soft to hard pellets as early as 1201 hours, or slightly before (Fig. 3). Female black-tails tended to initiate the same transition later in the afternoon. The earliest noted transition for a female was 1335 hours and most females initiated the transition between 1400 to 1430 hours. Most males had completed the transition to hard pellets by 1330 hours, but one male had started as late as 1450 hours (Fig. 3). Two females had not initiated the early afternoon transition by 1500 hours. Feces in the rectum of two males were composed entirely of hard pellets as early as 1408 hours and 1414 hours, respectively. No females had fully replaced the soft pellets in the rectum with hard pellets by 1500 hours.

The findings presented here generally support those reported by other authors (Spencer 1955, Watson and Taylor 1955, Lechleitner 1957, Hansen and Flinders 1969). Spencer (1955) found half the animals killed from 0900 hours to 1700 hours had soft pellets in their stomachs. There was evidence of soft pellets in stomachs of 21 of 25 animals killed at 1300 hours (Spencer 1955). Soft pellets were produced in all black-tailed jackrabbits collected from 0800 hours to 1000 hours in California, with evidence of the hares starting to reingest them (Lechleitner 1957). Amorphous pellets of the European hare (*Lepus europaeus*) were found in the recta of hares killed between 0600 hours and 1600 hours; all animals killed between 0800 hours and 1200 hours contained soft pellets in their recta (Watson and Taylor 1955). Lechleitner (1957) reported soft feces being produced and swallowed during the daylight hours, starting at 0600 hours and being replaced by hard feces by 2000 hours. However, the exact time of death was not known for the black-tails used in the sample, and sample sizes were minimal during the early morning hours. With the knowledge of the exact time of death, the periods of transition in pellet types in the black-tailed jackrabbit were more precise in our study. Lechleitner (1957), in reporting the cycle of reingestion and production of soft pellets in the black-tailed jackrabbit in California, found the period of occurrence of soft pellets in the rectum may extend to as late as 2000 hours. Our findings do not support his conclusion. We suggest that, although pellets may be found in the rectum as late as 1600 hours or 1700 hours, the transition to hard pellets in the afternoon is essentially completed by 1330 hours for males and 1430 hours for female black-tails. Our data support the theory that males begin the transition from hard to soft pellets earlier in the morning than do females. This relationship was significant ($P < 0.05$) using the Mann-Whitney-Wilcoxon 2-independent sample procedure. Females initiated the transition from soft to hard feces significantly later ($P < 0.01$) in the afternoon than males. Lechleitner (1957) found no evidence that indicated any seasonal trend of reingestion in the black-tailed jackrabbit. Thus, this relationship may in fact be a yearlong phenomenon.

The stimulus-response mechanisms causing the apparent dimorphism in behavioral physiology between the sexes is not known. However, reasons why this occurs may include partitioning of temporal feeding activities to reduce intersexual competition. This may be especially critical near the end of the winter season when forage above the snow level may be limiting, and when females are in late gestation or lactating. Intraspecific competition is maximal under peaking population cycles as well as during climatic seasons of stress. Intersexual segregation of temporal feeding cycles may tend to reduce this competition. Because of the higher energy requirements of gestation and lactation, female black-tails may feed later into the morning hours than males. Lactating females may suckle leverets in the early morning hours, and this demanding activity may help delay the production of soft pellets. In addition, females may reingest soft pellets later into the afternoon than males, thereby maximizing feeding efficiency and digestability of ingested forage.

Acknowledgments

We sincerely thank the following for their time, effort, and private funding so graciously donated to the collection of jackrabbits for this study: D. A. Barnum, J. S. Castrale, F. V. Luke, S. I. Steigers, and especially C. L. Elliott. We also thank H. Cheung for manuscript preparation and J. S. Castrale for his critical review of this manuscript. Figures were drawn by S. I. Steigers and N. P. Hebbert.

Literature Cited

Black, C. A., D. C. Evans, J. L. White, and others. 1965. Methods of soils analysis. Part I, Agronomy No. 9., Am. Soc. Agron. and Am. Soc. Testing Mater., Madison, Wisconsin. 802 pp.

Eden, A. 1940. Origin of night feces. Nature 145:628–629.

Griffiths, M., and D. Davies. 1963. The role of soft pellets in the production of lactic acid in the rabbit stomach. J. Nutr. 80:171–180.

Hansen, R. M., and J. T. Flinders. 1969. Food habits of North American hares. Sci. Ser. No. 1, Colorado State Univ., Fort Collins. 18 pp.

Herndon, J. E., and E. L. Hove. 1955. Surgical removal of the cecum and its effect on digestion and growth in rabbits. J. Nutr. 57:261–270.

Huang, T. C., H. E. Ulrich, and C. M. McCay. 1954. Antibiotics, growth, food utilization, and the use of chromic oxide in studies on rabbits. J. Nutr. 54:621–630.

Kulwich, R., L. Struglia, and P. B. Pearson. 1953. The effect of coprophagy on the excretion of B vitamins by the rabbit. J. Nutr. 49:639–645.

Lechleitner, R. R. 1957. Reingestion in the black-tailed jack rabbit. J. Mammal. 38:481–485.

Meyer, K. 1955. Coprophagy in the European rabbit (*Oryctolagus cuniculus*) in Australia. Austr. J. Zool. 3:336–345.

Morot, C. 1882. Des pelotes stomacales des leporides. Mem. Soc. Centr. Med. Vet. 12:137. *In* J. S. Watson. 1954. Reingestion in the wild rabbit, *Oryctolagus cuniculus* (L.). Proc. Zool. Soc. Lond. 124:615–624.

Olsen, H. M., and H. Madsen. 1944. Investigations on pseudorumination in the rabbit. Vidensk. Medd. fra Dansk natrh. Foren. 107:37. *In* E. J. Thacker and C. S. Brandt. 1955. Coprophagy in the rabbit. J. Nutr. 55:375–385.

Southern, H. N. 1942. Periodicity of refection in the wild rabbit. Nature 149:553–554.

Spencer, J. L. 1955. Reingestion in three American species of Lagomorphs. Lloydia. 18:197–199.

Thacker, E. J., and C. S. Brandt. 1955. Coprophagy in the rabbit. J. Nutr. 55:375–385.

Tiemeier, O. W. 1965. Bionomics. Pages 5–40 *in* C. P. Wilson, director, The black-tailed jack rabbit in Kansas. Kansas State Univ., Ag. Exp. Sta. Tech. Bull. 140. 75 pp.

Watson, J. S., and R. H. Taylor. 1955. Reingestion in the hare *Lepus europaeus*. Pol. Sci. 121:314.

PRAIRIE DOG COLONY ATTRIBUTES AND ASSOCIATED VERTEBRATE SPECIES

Tim W. Clark[1], Thomas M. Campbell III[2], David G. Socha[3], and Denise E. Casey[2]

Abstract.— A survey of colony attributes and associated vertebrates on black-tail (*Cynomys ludovicianus*), Gunnison's (*C. gunnisoni*), and white-tail (*C. leucurus*) prairie dogs was made. A belt transect 1.6 km wide and 13,334 km long from Hobbs, New Mexico, to the Utah-Wyoming state line was surveyed. There were 47 colonies located (4760 ha comprising 2.2 percent) in the belt. Intercolony distances varied significantly. Three black-tail towns averaged 33 ha in area (SD = 26, range 10–61), 11 Gunnison's averaged 46 ha (SD = 43, range 16–150), and 33 white-tail towns averaged 125 ha (SD = 200, range 0.2–958). Badger activity was positively and significantly correlated to colony size and number of burrow openings on Gunnison's and white-tail towns. There were 107 vertebrate species and subspecies (one amphibian, 25 reptiles, 51 birds, 30 mammals) observed on prairie dog colonies. Results of our surveys are compared with prairie dog studies elsewhere. The role of prairie dogs and relationships to some vertebrates species are discussed.

This paper describes results of a survey of colony characteristics and associated vertebrate species for three prairie dog species in Utah, Colorado, and New Mexico.

Study Area

Prairie dog colonies surveyed were in a belt transect (1.6 km wide and 1334 km long) beginning near Hobbs, New Mexico, and ending on the Utah-Wyoming state line (Fig. 1). The transect generally followed an existing pipeline corridor. The prairie dog species encountered were: black-tail (*Cynomys ludovicianus*), Gunnison (*C. gunnisoni*), and white-tail (*C. leucurus*). These species collectively occupied many vegetation-physiographic types. Overall, black-tail colonies were in shortgrass prairie with *Bouteloua* sp. and *Buchloe dactyloides* with scattered *Opuntia imbricata*. Gunnison colonies were associated with *Juniperus monosperma*, shrubs, and *O. imbricata*, as well as a variety of forbs and grasses. White-tail colonies had an overstory of *Artemisia* sp. and a diverse understory of forbs and grasses.

Methods

All prairie dog colonies were aerially located and mapped onto U.S. Geological Survey 7.5 and 15 minute maps. Beginning in June 1980, near Hobbs, New Mexico, and working north to Wyoming, each town was visited, precisely mapped, and inventoried in detail. Surveys followed guidelines designed for black-footed ferret (*Mustela nigripes*) searches (Clark and Campbell, in preparation), and allowed for a concomitant general survey of vertebrate species.

Diurnal surveys began with a 1-hr observation of the colony with binoculars and spotting scopes from vantage points. Similar predusk observation periods were also conducted. Walking surveys were made immediately following morning surveys. Each colony was thoroughly walked by up to 12 people simultaneously. Each person moved back and forth within a 30 m wide area and examined all prairie dog burrow openings, mounds, and adjacent areas, as well as the overall surface of the colony. Each burrow examined was marked with a footprint to assure complete, nonoverlapping coverage. Data recorded included: number of burrow openings (5 cm or larger in diameter); number of burrow openings in "active" use, where possible to determine; number of badger excavated holes; number of plugged burrow openings; number of km walked;

---

[1] Department of Biology, Idaho State University, Pocatello, Idaho 83209.
[2] Biota Research and Consulting, Inc., P.O. Box 2705, Jackson, Wyoming 83001.
[3] Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706.

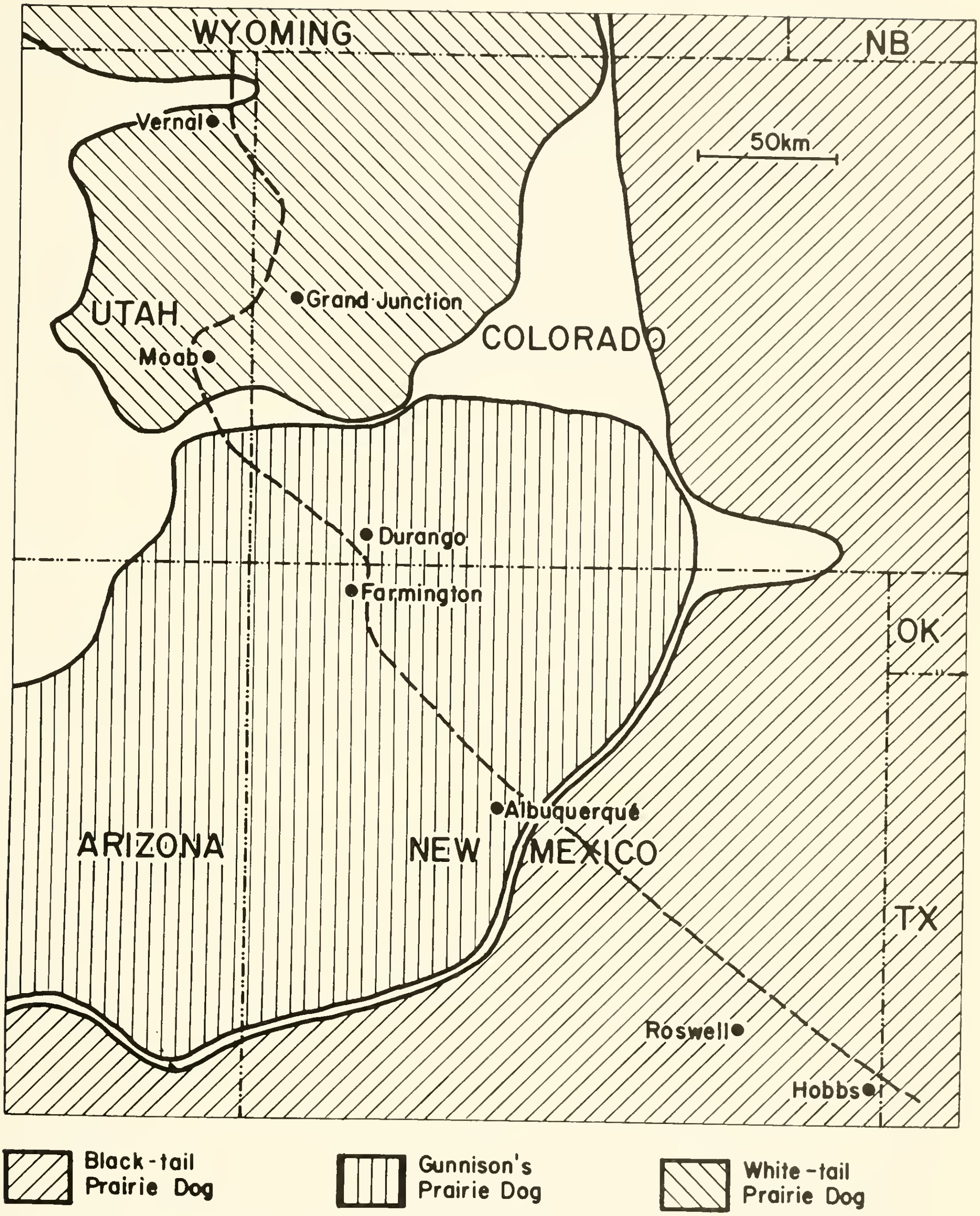

WYOMING
NB
Vernal
50km
UTAH
Grand Junction
COLORADO
Moab
Durango
Farmington
OK
ARIZONA
NEW MEXICO
Albuquerque
TX
Roswell
Hobbs
Black-tail Prairie Dog
Gunnison's Prairie Dog
White-tail Prairie Dog

Fig. 1. Map of the three prairie dog species' distribution along the belt transect study area (dotted line) in New Mexico, Colorado, and Utah.

time spent walking; and number and species of all live vertebrates and their remains seen. Since badgers are considered the single most effective predator and directly alter a colony by digging, badger activity (percentage of burrows enlarged by badgers) was estimated on each colony (Campbell and Clark 1981).

Nocturnal surveys of prairie dog colonies were conducted via spotlighting. Two spotlights were used simultaneously by each crew of two persons. One cab-mounted light was used by the driver and the second, hand-held light was used by the rider seated in back. The spotlights generally allowed identification of animals out to 150 m as the truck moved at 3–8 km/hr. Travel time around a spotlight circuit varied in relation to colony size and terrain, but was usually 15–60 minutes. On small towns (less than 10 ha) a single stationary spotlighting location was used. Spotlighting was started just after sunset and continued until around midnight and again from about 0300 hours till sunrise. All colonies were spotlighted for at least three consecutive nights, but large towns were spotlighted longer. All animals seen were identified to species and numbers recorded.

To compare the two nighttime survey periods for vertebrate activity and inter-observer differentials, all vertebrates seen were lumped into classes based on taxonomy and morphology (primarily body size): (1) lagomorphs, (2) rodents, (3) flying vertebrates (birds and bats), (4) small carnivores (badgers and smaller forms), (5) large carnivores (coyotes and bobcats), and (6) ungulates. Lagomorphs, rodents, and flying vertebrates were compared between number of species seen on the first spotlight circuit of the post-sunset and predawn survey periods. All other classes were compared on number of species seen per hour over the entire survey periods.

RESULTS

Prairie Dog Colony Attributes

The 47 prairie dog colonies located totaled 4760 ha and comprised 2.2 percent of the belt transect (Table 1). Black-tails occupied 0.04 percent of the transect, Gunnison colonies 0.2 percent, and white-tail colonies 1.9 percent. Gunnison and white-tail colonies were clumped in distribution; information was insufficient to determine if black-tail colonies were also clumped.

The first three colonies encountered were black-tails, and intercolony distances between colony 1 and 2 and between 2 and 3 was 6.4 km and 86.3 km, respectively. Distance to the next colony, a Gunnison town, was 355 km. Gunnison colonies fell into four distinct clumps; 127 km separated the first (N = 6 towns) and second (N = 2 towns) clumps, 30.6 km the second and third (N = 2), and 245.5 km the third and fourth (N = 1).

TABLE 1. Comparative colony characteristics among the clumps of prairie dog colonies by prairie dog species.

			Prairie
Colony characteristics	Black-tails		Gunn-
	Clump 1	Clump 1	Clump 2
Location	NW New Mexico		
Number of colonies	3	6	2
Total area (ha)	99	235	116
Colony area (ha):			
Mean (SD)	33(26)	39(27)	58(15)
Range	10–61	3–73	47–69
x̄ Intercolony distance (km)	46.4	2.3	3.2
Total burrow openings	2763	5238	1004
Burrow openings/ha:			
Mean (SD)	32.5(8.9)	209(8.4)	8.8(0.9)
Range	23.9–41.7	8.2–32.0	8.1–9.4
Plugged burrows: Number and % of all openings	106(3.8%)	13(0.2%)	4(0.3%)
Badger reamed: Number and % of total openings	102(3.4%)	366(7.8%)	65(6.8%)
Vertebrate skeletal remains:			
Prairie dogs/ha	0.273	0.196	0.078
Other species/ha	0.131	0.008	0.008
Vegetation (cm):			
x̄ Height (SD)	64(23)	79(29)	46(22)
Range	51–91	38–112	30–61

The mean intercolony distance for Gunnison colonies ($N = 10$) was 2.4 km ($SD \pm 1.6$) range 0.5–5.3. The 33 white-tail colonies were distributed in two clumps. The first group of 15 towns was about 96 km from the nearest Gunnison colony and 115 km from the second white-tail colony group ($N = 18$). Mean intercolony distance for white-tails was 4.9 km ($SD \pm 3.0$) range 0.8–11.3. Intercolony distances varied significantly interspecifically ($F_{2,37} = 17.92$, $P < 0.01$) and intraspecifically for white-tails ($X^2 = 56.14$, $df = 31$, $P < 0.005$).

The interspecific size of prairie dog colonies varied, but insignificantly ($F_{2,44} = 1.13$, $P > 0.05$). Three black-tail colonies had a mean size of 33 ha ($SD \pm 26$) range 10–61, 11 Gunnison towns averaged 46 ha ($SD \pm 43$) range 1.6–150, and 33 white-tail colonies averaged 125 ha ($SD \pm 200$) range 0.2–958. A significant difference ($P < 0.05$) in mean colony size was evident within each of the three prairie dog species (black-tails $X^2 = 40.44$, $df = 2$; Gunnisons, $X^2 = 404.21$, $df = 10$; white-tails, $X^2 = 10245.69$, $df = 32$).

Plugged burrows were found in colonies of all three species. Black-tails showed 3.8 percent plugged of 2763 burrow openings, Gunnisons 0.3 percent of 8987 and white-tails 1.0 percent of 85,572. The interspecific density of burrow openings per colony varied insignificantly ($F_{2,44} = 1.09$, $P > 0.10$) among the three species, with black-tails showing 27.9/ha ($SD \pm 8.6$, range 24–41.3), Gunnisons 17.6/ha ($SD \pm 49.2$, range 8.2–179), and white-tails with 21/ha ($SD \pm 29.2$, range 2.2 = 158).

All colonies showed signs of badger activity in the form of excavated holes and scats. Badger-reamed prairie dog holes (holes suspected of being enlarged by badger digging) on colonies varied significantly between the three prairie dog species ($F_{2,44} = 4.67$, $P < 0.05$). Badger activity was significantly lower on black-tail colonies than on Gunnison ($t = -7.42$, $df = 12$, $P < 0.01$) and white-tail colonies ($t = -8.69$, $df = 34$, $P < 0.01$), but was not significantly different on Gunnison and white-tail colonies ($t = -1.88$, $df = 42$, $P > 0.10$). Badger activity was positively and significantly correlated ($P < 0.01$) to colony size and to the number of burrow openings on each colony for both Gunnisons ($r = 0.8729$, $t = 5.37$ and $r = 0.9431$, $t = 8.51$, respectively) and white-tails ($r = 0.9084$, $t = 12.10$ and $r = 0.9845$, $t = 31.25$, respectively), but not for black-tails, nor were there

Table 1 continued.

dog species					
ison's			White-tails		
Clump 3	Clump 4	Total	Clump 1	Clump 2	Total
SW Colorado	E Utah	–	E Utah		–
2	1	11	15	18	33
10	150	511	566	3584	4150
5(4)	150	33(26)	38(37)	199(249)	125(200)
2–8	–	2–73	9–121	0.2–958	0.2–958
1.6	–	2.4	5.5	4.4	4.9
668	2077	8987	8993	76,579	85,572
96.2(69.1)	13.8(–)	31.7(39.4)	19.8(10.3)	30.8(37.6)	25.8(28.8)
47.3–145	–	8.1–145	2.3–40.5	5.1–160	2.3–160
0	8(0.4%)	25(0.3%)	23(0.3%)	40(0.3%)	790(0.9%)
50(7.2%)	235(11.3%)	716(7.8%)	769(9.3%)	16,469(17.5%)	17,238(13.8%)
0.90	0.287	0.209	0.150	0.159	0.157
0.30	0.012	0.018	0.0179	0.0209	0.020
84(32)	61	673(28)	39(23)	46(15)	42.6(19)
61–107	–	30–112	0–91	15–71	0–91

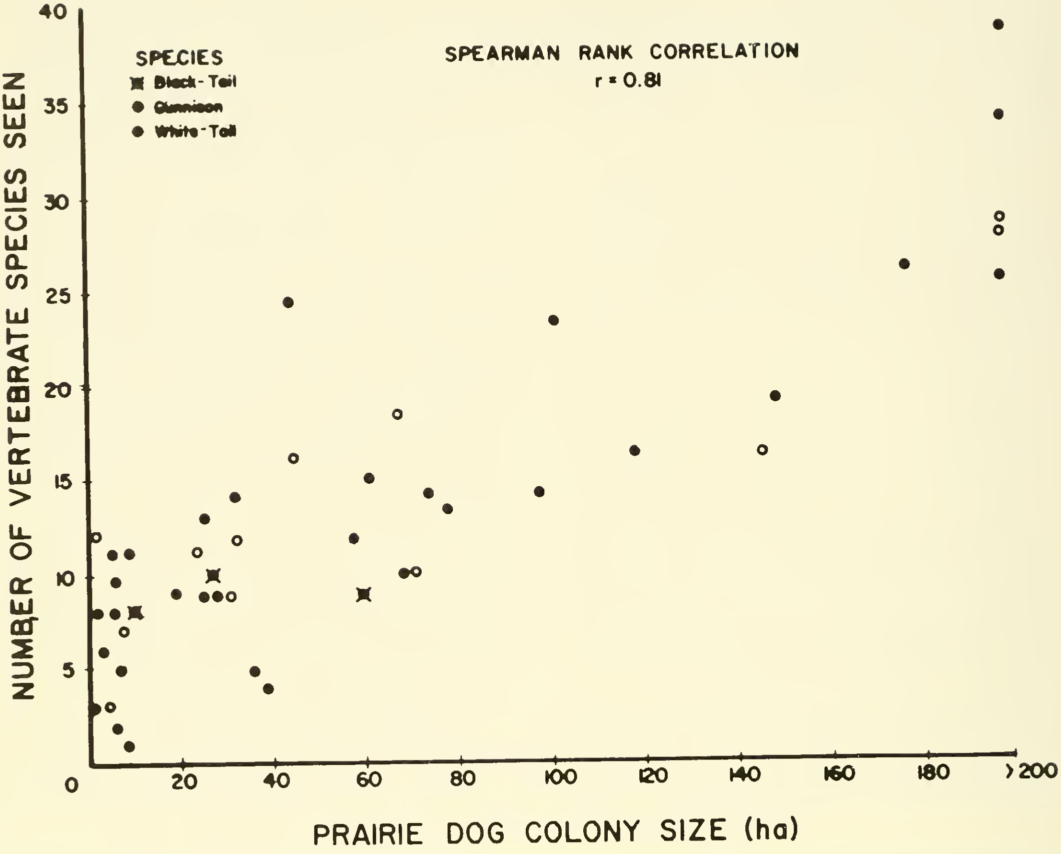


Fig. 2. Relationship between black-tail, Gunnison, and white-tail prairie dog colony size and number of vertebrate species observed on each colony.

significant correlations with burrow density or intercolony distances.

Associated Vertebrate Species

A total of 107 species and subspecies, vertebrate animals, including one amphibian, 25 reptiles, 51 birds, and 30 mammals, were observed on prairie dog colonies (Table 2). A larger number of vertebrate species were seen on white-tailed colonies than on colonies of the other two prairie dog species; 88 percent of the surface area of all prairie dog colonies was in white-tail colonies.

Six species of mammals, 7 species of birds, 2 species of reptiles, and no species of amphibians were common to colonies of all three prairie dog species. In contrast, 7 mammal, 11 bird, 8 reptile, and no amphibian species were common to colonies of two prairie dog species, and 17 mammal, 33 bird, 15 reptile, and one amphibian species were present on colonies of only one prairie dog species.

The relationship between the number of vertebrate species seen on prairie dog colonies of varying sizes is shown in Figure 2. A Spearman Rank Correlation ($r = .81$) showed that larger towns contained more vertebrate diversity than smaller colonies.

Four rattlesnake species and subspecies were found, 1 western diamondback, 4 Hopi, 7 prairie, and 6 midget-faded rattlesnakes. Rattlesnakes on black-tail colonies occurred at 0.02/ha, on Gunnison at 0.02/ha, and on white-tail at 0.002/ha. The Hopi were on a single 148 ha Gunnison colony.

Eleven raptor species, including one eagle, 4 hawks, 3 falcons, and 3 owls, were seen. Burrowing owls ($N = 99$) occurred on 19 towns and at a density of 0.04 owls/ha. The greatest density was 15 owls on a 10 ha town.

TABLE 2. Vertebrate species and subspecies observed on the colonies of three prairie dog species in New Mexico, Colorado, and Utah.

Vertebrate species and subspecies	Prairie dog species		
	Black-tail	Gunnison	White-tail
AMPHIBIANS			
Great Basin spadefoot toad (*Scaphiopus intermontanus*)			X
Totals	0	0	1
REPTILES			
Mountain short-horned lizard (*Phrynosoma douglassi hernandesi*)			X
Eastern short-horned lizard (*P. douglassi brevirostre*)			X
Desert short-horned lizard (*P. douglassi ornatissimum*)		X	X
Texas horned lizard (*P. cornutum*)	X		
Sagebrush lizard (*Sceloporus grasiosus*)	X	X	X
Northern plateau lizard (*S. undulatus elongatus*)			X
Northern whiptail (*Cnemidophorus tigris septentrionalis*)			X
Western whiptail (*C. tigris*)		X	X
Little striped whiptail (*C. inornatus*)	X	X	
Chihuahua whiptail (*C. exsanguis*)	X	X	
Checkered whiptail (*C. tesselatus*)		X	
Leopard lizard (*Crotaphytus wislizenii*)			X
Lesser earless lizard (*Holbrookia maculata*)	X	X	X
Side-blotched lizard (*Uta stansburiana*)		X	X
Western coachwhip (*Masticophis flagellum testaceus*)		X	
Great Basin gopher snake (*Pituophis melanoleucus deserticola*)		X	X
Bullsnake (*P. m. sayi*)		X	
Utah milk snake (*Lampropeltis triangulum taylori*)			X
Wandering garter snake (*Thamnophis elegans vagrans*)			X
Painted desert glossy snake (*Arizona elegans philipi*)		X	
Western diamondback rattlesnake (*Crotalus atrox*)		X	
Midget faded rattlesnake (*C. viridis concolor*)		X	X
Prairie rattlesnake (*C. v. viridis*)	X	X	
Hopi rattlesnake (*C. v. nuntius*)		X	
Western box turtle (*Terrapene ornata*)	X		
Totals (n = 25)	6	16	15
BIRDS			
Canada Goose (*Branta canadensis*)			X
Mallard (*Anas platyrhynchos*)			X
Green-winged Teal (*Anas crecca*)			X
Turkey Vulture (*Cathartes aura*)			X
Marsh Hawk (*Circus cyaneus*)			X
Red-tailed Hawk (*Buteo jamaicensis*)		X	X
Ferruginous Hawk (*B. regalis*)	X	X	X
Swainson's Hawk (*B. swainsoni*)	X		
Golden Eagle (*Aquila chrysaetos*)			X
Prairie Falcon (*Falco mexicanus*)			X
Merlin (*F. columbarius*)			X
Kestrel (*F. sparverius*)	X	X	X
Short-eared Owl (*Asio flammeus*)			X
Great Horned Owl (*Bubo virginianus*)			X
Burrowing Owl (*Athere cunicularia*)	X	X	X
Sage Grouse (*Centrocercus urophasianus*)			X
Gambel's Quail (*Lophortyx gambelii*)		X	
Killdeer (*Charadrius vociferus*)		X	X
Western Sandpiper (*Calidris mauri*)			X
Mourning Dove (*Zenaida macroura*)	X	X	X
Common Nighthawk (*Chordeiles minor*)		X	X
Lesser Nighthawk (*C. acutipennis*)		X	X
Poor-will (*Phalaenoptilus nuttallii*)			X

Table 2 continued.

Vertebrate species and subspecies	Prairie dog species		
	Black-tail	Gunnison	White-tail
BIRDS continued.			
Western Kingbird (*Tyrannus verticalis*)		X	X
Say's Phoebe (*Sayornis saya*)		X	X
Gray Flycatcher (*Empidonax wrightii*)			X
Ash-throated Flycatcher (*Myiarchus cinerascens*)		X	
Horned Lark (*Eremophila alpestris*)	X	X	X
Violet-green Swallow (*Tachycineta thalassina*)			X
Barn Swallow (*Hirundo rustica*)			X
Rough-winged Swallow (*Stelgidopteryx ruficollis*)			X
Pinyon Jay (*Gymnorhinus cyanocephalus*)		X	
Black-billed Magpie (*Pica pica*)			X
Common Raven (*Corvus corax*)		X	X
Rock Wren (*Salpinctes olsoletus*)			X
Sage Thrasher (*Oreoscoptes montanus*)		X	X
Curve-billed Thrasher (*Toxostoma curvirostre*)	X		
Mockingbird (*Mimus polyglottos*)		X	X
Mountain Bluebird (*Sialis currucoides*)		X	X
Northern Shrike (*Lanius excubitor*)			X
Loggerhead Shrike (*L. ludovicianus*)			X
Western Meadowlark (*Strunella neglecta*)	X	X	X
Eastern Meadowlark (*S. magna*)		X	
Brewer's Blackbird (*Euphagus cyanocephalus*)			X
Western Tanager (*Piranga lucoviciana*)			X
Grasshopper Sparrow (*Ammodramus savannarum*)			X
Vesper Sparrow (*Pooecetes gramineus*)			X
Black-throated Sparrow (*Amphispiza bilineata*)		X	
Sage Sparrow (*A. belli*)		X	X
Lark Sparrow (*Chondestes grammacus*)	X	X	X
Brewer's Sparrow (*Spizella breweri*)			X
Totals (n = 51)	9	23	44
MAMMALS			
Bat (unidentified)		X	X
Desert cottontail (*Sylvilagus auduboni*)	X	X	X
Mountain cottontail (*S. nuttalli*)		X	X
White-tailed jackrabbit (*Lepus townsendi*)			X
Black-tailed jackrabbit (*L. californicus*)	X	X	X
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	X		X
Wyoming ground squirrel (*S. elegans*)			X
Whitetail antelope squirrel (*Ammospermophilus leucurus*)		X	
Pocket gopher (*Thomomys* sp.)		X	
Valley pocket gopher (*T. bottae*)			X
Plains pocket gopher (*Geomys bursarius*)	X		
Least chipmunk (*Eutamius minimus*)			X
Woodrat (*Neotoma* sp.)		X	
Bushytail woodrat (*N. cinerea*)			X
Southern plains woodrat (*N. micropus*)	X		
Ord kangaroo rat (*Dipodomys ordi*)	X	X	X
Bannertail kangaroo rat (*D. spectabilis*)		X	
Deer mouse (*Peromyscus maniculatus*)			X
Vole (*Microtus* sp.)			X
Muskrat (*Ondatra zibethica*)			X
Coyote (*Canis latrans*)	X	X	X
Swift fox (*Vulpes velox*)		X	X
Domestic dog (*Canis familiarus*)		X	X
Domestic cat (*Felis domesticus*)		X	
Long-tailed weasel (*Mustela frenata*)	X		X

Table 2 continued.

Vertebrate species and subspecies	Prairie dog species		
	Black-tail	Gunnison	White-tail
MAMMALS continued.			
Short-tailed weasel (*M. erminea*)			X
Badger (*Taxidea taxus*)	X	X	X
Striped skunk (*Mephitis mephitis*)			X
Mule deer (*Odocoileus hemionus*)		X	X
Pronghorn (*Antilocapra americana*)	X	X	X
Totals (n = 30)	10	16	23

Only two live weasels were found, a bridled weasel in New Mexico (61 ha town) and a short-tailed weasel in Utah (102 ha town). Both were sighted in daylight.

Fourteen live badgers were seen on 10 colonies (1 badger/183 ha, range 0.2–522). All badgers were the sole mustelid species seen on its respective town except for 5 badgers on a 946 ha town (1 badger/189 ha). All towns showed signs of badger activity, although varying greatly in density.

Coyotes (N = 29) were seen on 18 towns (1 coyote/115 ha). An additional 12 towns had coyote scats. Kit foxes (N = 5) were seen on 4 towns that had a mean size of 62 ha (range 20–148). Two foxes were on a 26 ha town.

Numerous vertebrate remains were found on prairie dog towns (Table 1). In all, 1597 remains of individual prairie dogs and 202 other vertebrate remains of at least 16 species were found. Prairie dog remains occurred at about one skeleton/5 ha and remains of other vertebrates at about 1/50 ha.

Nocturnal survey results showed that some vertebrates had a differential observability between the postsunset and predawn survey periods. The front and back spotlight personnel observed species and categories of vertebrates differentially. Three categories of vertebrate sightings—flying forms ($X^2 = 159$, df = 1, $P < 0.01$), ungulates ($X^2 = 11$, df = 1, $P < 0.01$), and large carnivores ($X^2 = 10.5$, df = 1, $P < 0.05$)—showed significant differences in observability, which may reflect real differences in activity, with most being seen per unit effort in postsunset periods.

Rodents ($X^2 = 18.8$, df = 1, $P < 0.01$) and flying vertebrates ($X^2 = 45.1$, df = 1, $P < 0.01$) were sighted significantly more by the driver than the rider in back. The driver and rider saw no significant differences between all other classes.

DISCUSSION

Prairie dog colonies occupied only a small portion of the survey area (2.2 percent); less than 1 percent for black-tail and for Gunnison and about 1.9 percent for white-tail. The U.S. Forest Service (1981) found black-tails on Thunder Basin National Grassland, Wyoming, to occupy 1.3 percent. Elsewhere in Wyoming, Campbell and Clark (1981) found black-tails to occupy only 0.7 percent of a 1036 km^2 and white-tails 3.2 percent of 336 km^2. An area in southwest Wyoming contained 63 white-tail towns and occupied 25 percent of the 259 km^2 area (Clark and Campbell, unpubl. ms.). White-tails in two other areas in southern Wyoming occupied 7.2 percent and 8.9 percent of the study area (Martin and Schroeder 1979, 1980) (Table 3).

In comparing the three black-tail colonies in our study with 186 other black-tail towns elsewhere, our 11 Gunnisons with one other, and our 33 white-tail towns with 354 others (Table 3), all the towns we surveyed fall within the ranges of colony sizes and burrow opening features previously reported. Our survey of Gunnison prairie dogs appears to be the first relatively large sample. We found a mean intercolony distance of 46.4 km for black-tails, 2.4 km for Gunnisons and 4.9 km for white-tails, whereas Campbell and Clark (1981) found 4.7 km (SD ± 2.7) range 1.6–11.3 for white-tails in two large relatively undisturbed areas in Wyoming.

Prairie dog colonies were found clumped in suitable habitat, and nearby colonies served as sources for colonizing animals. White-tail colonies (N = 19) in the Vernal, Utah, clump were part of a much larger complex of colonies estimated to be at least 5,000 ha. No comparable situation for the black-tail or Gunnison was found.

Prairie dogs are known to plug burrows in response to predator investigations, death of prairie dogs, and other disturbances (Koford 1958, Henderson et al. 1969). We found black-tails plugged 3.8 percent of their burrow openings, Gunnisons 0.2 percent and white-tails 0.9 percent. In comparison, Campbell and Clark (1981) found 0.0005 percent plugged burrow openings for black-tails and 0 percent for white-tails in Wyoming.

Gold (1976), Bonham and Lerwick (1976), and Hansen and Gold (1977) noted that black-tail prairie dogs manipulate soil and increase plant and animal density and therefore may be viewed as ecosystem regulators. Uresk and Bjugstad (in press) noted that peak plant production of aboveground herbage over their five-year study occurred where prairie dogs only grazed during the last four years of the study, rather than under the other comparative treatments (prairie dogs and steers, steers only, neither).

Our surveys found 107 vertebrate species and subspecies on or over prairie dog colonies. Additional species occupying prairie dog colonies were reported by Tyler (1968), Martin and Schroeder (1979, 1980), and Campbell and Clark (1981). Collectively, over 140 vertebrate species have been reported associated with prairie dogs.

A general account of many of the more conspicuous vertebrates and their interrelationships with prairie dogs was discussed by Koford (1958). Prairie dogs improve habitat for prairie animals that are benefited by holes, unvegetated areas, and short vegetation and for those that feed on prairie dogs. The prairie dog burrow is a critical element in prairie dog survival and allows them to escape the extremes of temperature, for example, and benefits numerous other vertebrates as well (Stromberg 1978). Desert cottontails, burrowing owls, swift foxes, rattlesnakes, and some species of plants are enhanced by prairie dog activities (Uresk and Bjugstad, in press). Sixty-three percent more small mammals, other than prairie dogs, were live-trapped on pastures used by steers and prairie dogs than on steer-only pastures (O'Melia 1980). O'Melia also found prairie dogs significantly decrease arthropod populations.

Table 3. Prairie dog colony characteristics for black-tail, white-tail, and Gunnison prairie dog species found in this and other studies conducted in Wyoming, Colorado, Montana, Kansas, and South Dakota.

Prairie dog species and location	Number of colonies	Colony area (ha)	
		Total	x̄ (SD) range
Black-tail Prairie Dog			
Southeast New Mexico	3	99	33(26)10–61
Central Wyoming	21	731	35(44)1–189
Eastern Wyoming	2	123	66(--)26–97
Central South Dakota	151	1,283	8.5(--)--
Western South Dakota	2	—	--(--)--
Northern Colorado	1	3	3(--)--
Great Plains	—	—	--(--)--
Central Kansas	1	47	47(--)--
Northern Wyoming	7	580	83(--)2.8–359
Gunnison Prairie Dog			
Northeast New Mexico	11	511	33(26)2–73
Southwest Colorado	1	6	6(--)--
White-tail Prairie Dog			
Eastern Utah	33	4,150	125(200)0.2–958
South central Wyoming	25	1,085	43(46)2–184
Northwest Wyoming	4	3,055	764(--)121–1416
Southwest Wyoming	63	3,992	63(--)0.4–671
South central Wyoming	1	13	13(--)--
Southern Wyoming	164	4,006	24(--)0.8–510
Southern Wyoming	81	60,665	54(--)0.4–414
Southern Montana	15	285	19(--)----
North central Colorado	1	9	9(--)--

Prairie dogs provide food to the black-footed ferret (Hillman and Clark 1980), badgers, foxes, coyotes, bobcats, and weasels as well as to Golden Eagles, Ferruginous Hawks, and Swainson's Hawks (Campbell and Clark 1981). The U.S. Bureau of Land Management (1979) noted that prairie dog towns also provide nest sites for Mountain Plovers (*Charadrius montanus*) and McCown's Longspur (*Calcarius mccownii*) and benefit other birds such as Killdeer, Eastern Kingbirds (*Tyrannus tyrannus*), Upland Sandpiper, Long-billed Curlews (*Numenius americanus*) and Mourning Doves, to mention a few. Sharp-tailed (*Pedioecetes phasianollus*) and Sage grouse sometimes strut on prairie dog towns (McEneany and Jensen 1974). A large number of reptiles use prairie dog holes for thermoregulation and protection from predators. Reptiles eat arthropods inhabiting both burrows and the surface of the colony (Wilcomb 1954, Clark 1977).

Evidence of human presence—roads, spent shell casings, plowing, and some evidence of poisoning—was obvious on many colonies. Our observations in this study and elsewhere indicate that most prairie dog colonies are negatively influenced by humans; only a few areas still contain large, relatively undisturbed colonies.

This brief account of prairie dog colony attributes and the relationships of some associated vertebrate species with prairie dogs shows that numerous benefits may be accrued to some of those vertebrates. Prairie dog colonies may constitute peaks in species diversity and biomass for small vertebrates found nowhere else in the prairie ecosystem. Needed are precise community ecology studies, with adequate controls near prairie dog towns, to quantify relative degrees of association between the various vertebrate species and prairie dogs and to identify the types of relationships that exist.

ACKNOWLEDGMENTS

Many people provided direct aid to this project. James Leiber and Gene Bell of Mid-America Pipeline Co., Inc., Tulsa, Oklahoma, provided the opportunity and support for the survey. Dana Shuford, U.S. Bureau of Land

Table 3 continued.

Burrow openings				
	Density/ha			
Total	x̄ (SD) Range	Percent plugged	Percent badger reamed	Sources
2,763	33(9)24–42	3.8	3.4	This study
17,095	21(24)11–67	0.0	10.0	Campbell & Clark 1981
6,015	49(10)38–52	0.9	2.6	Clark & Campbell unpubl.
—	—(——)—	—	—	Linder et al. 1972
—	135(——)131–140	—	—	King 1955
289	96(——)—	—	—	Tileston & Lechleitner 1966
—	5(——)15–67	—	—	Koford 1958
6,344	135(——)—	—	—	Smith 1958
29,215	50(——)—	2.2	—	Martin & Schroeder 1980
8,987	32(39)8–145	2.8	7.8	This study
321	57(——)—	—	—	Fitzgerald & Lechleitner 1974
85,572	26(29)2–160	0.9	13.8	This study
27,779	25(26)9–129	0.0	27	Campbell & Clark 1981
6,755	2.2(——)1–6	—	—	Clark et al. unpubl.
168,761	42(——)0.7–21.3	—	24.7	Clark & Campbell unpubl. and Martin & Schroeder 1979, 1980
827	64(——)—	—	—	Clark 1977
105,497	26(——)0.8–41	—	—	Martin & Schroeder 1979
129,969	32(——)—	4.3	—	Martin & Schroeder 1980
—	—(——)—	—	—	Flath 1979
252	28(——)—	—	—	Tileston & Lechleitner 1966

Management, helped facilitate the project. Janice Hutton, David Hayden, and Ron Freeman of Woodward/Clyde Consultants, San Francisco, California, provided administrative and field assistance.

In addition to ourselves, survey teams consisted of Marcia Casey, Janette Johnson, Cheryl Lorenz, Suzanne Martell, Ronald Pace, Anne Rathbun, Sue Wandersee, JoAnn Camenzind, Marilyn McElheney, Kane Brightman, John Hoak, and Karen Jerger. Their untiring efforts, keen observations, and total commitment to a quality survey were invaluable. We would like to thank Jeff Marks for aiding with bird names. We sincerely thank all those people who directly aided in the survey and many others not mentioned by name who helped indirectly.

LITERATURE CITED

Bonham, D. C., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. J. Range Manage. 27:221–225.

Campbell, T. M., and T. W. Clark. 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. Am. Midl. Nat. 105:269–276.

Clark, T. W. 1977. Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*). Milwaukee Public Mus. Publ. Biol. Geol. No. 3. 97 pp.

Fitzgerald, J. P., and R. R. Lechleitner. 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. Am. Midl. Nat. 92:146–163.

Flath, D. L. 1979. Status of the white-tailed prairie dog in Montana. Proc. Mont. Acad. Sci. 38:63–67.

Gold, I. K. 1976. Effects of blacktail prairie dog mounds on shortgrass vegetation. Unpublished thesis. Colorado State Univ., Fort Collins, Colorado. 39 pp.

Hansen, R. M., and I. K. Gold. 1977. Blacktail prairie dogs, desert cottontails, and cattle trophic relations on shortgrass range. J. Range Manage. 30:210–214.

Henderson, F. R., P. F. Springer, and R. Adrian. 1969. The black-footed ferret in South Dakota. South Dakota Dept. Game, Fish, and Parks Tech. Bull. 4. 37 pp.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Univ. Michigan Contrib. Lab. Vert. Biol. 67:1–123.

Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildl. Monogr. No. 3. 78 pp.

Linder, R. L., R. B. Dahlgren, and C. N. Hillman. 1972. Black-footed ferret-prairie dog interrelationships. Pages 22–37 *in* Symp. Rare and Endangered Wildl. of the SW U.S., Sept. 22–23, 1972. Albuquerque, New Mexico.

Martin, S. J., and M. H. Schroeder. 1979. Black-footed ferret surveys on seven coal occurrence areas in southwestern and southcentral Wyoming, June 8 to September 25, 1978. Final report, Wyoming State Office BLM. 37 pp.

______. 1980. Black-footed ferret surveys on seven coal occurrence areas in Wyoming, February–September, 1969. Final report, Wyoming State Office BLM. 39 pp.

McEneany, T. P., and J. L. Jensen. 1974. Status of the black-tailed prairie dog on the Charles M. Russell National Wildlife Refuge. USFWS. Lewiston, Montana. 7 pp.

O'Melia, M. E. 1980. Competition between prairie dogs and beef cattle for range forage. Unpublished thesis. Oklahoma State Univ., Stillwater, Oklahoma. 33 pp.

Pizzimenti, J. J. 1981. Increasing sexual dimorphism in prairie dogs: evidence for changes during the past century. Southw. Nat. 26:43–47.

Smith, R. E. 1958. Natural history of the prairie dog in Kansas. Univ. Kans. Mus. Nat. Hist. and St. Biol. Surv. Misc. Publ., 16:1–36.

Stromberg, M. R. 1978. Subsurface burrow connections and entrance spatial pattern of prairie dogs. Southw. Nat. 23:173–180.

Tileston, J. V., and R. R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dog in north central Colorado. Am. Midl. Nat. 75:292–316.

Tyler, J. D. 1968. Distribution and vertebrate associates of the black-tailed prairie dog in Oklahoma. Unpublished dissertation. Univ. of Oklahoma, Norman, Oklahoma. 85 pp.

Wilcomb, M. J. 1954. A study of prairie dog burrow systems and the ecology of their arthropod inhabitants in central Oklahoma. Unpublished dissertation. Univ. of Oklahoma, Norman, Oklahoma. 154 pp.

Uresk, D. W., and A. J. Bjugstad. Effects of prairie dogs and cattle on the vegetation of the northern high plains. Proc. 7th No. Amer. Prairie Conf. (in press).

U.S. Bureau of Land Management. 1979. Habitat management plan-prairie dog ecosystem. Montana State Office, Billings, Montana. 61 pp.

U.S. Forest Service. 1981. Thunder Basin prairie dog management. USDA. Environmental Assessment. Thunder Basin Nat. Grasslands, 809 South 9th St., Douglas, Wyoming 82633.

DISTRIBUTION OF THE MOSS FAMILY GRIMMIACEAE IN NEVADA

Matt Lavin[1]

ABSTRACT.— Twenty-six taxa of Grimmiaceae are listed from Nevada, all representing the genera *Grimmia* and *Rhacomitrium*. *Rhacomitrium heterostichum* (Hedw.) Brid. var. *heterostichum* and *Grimmia atricha* C. Muell. & Kindb. ex Mac. & Kindb. are listed for the first time as occurring in Nevada. Within the state, the Mohave Desert, the Great Basin desert, and the Sierra Nevada display unique composition of members of the Grimmiaceae. *Grimmia anodon* is the most widespread moss in the state. Others, such as *Grimmia rivulare, G. conferta,* and *G. alpicola* inhabit only the montane environments of northeastern Nevada.

Nearly 1000 collection or observation sites throughout Nevada were visited during the past four years that the moss family Grimmiaceae has been under investigation. Two genera make up this family in Nevada, *Grimmia* and *Rhacomitrium*. *Schistidium*, in this paper, is used as a subgenus under the genus *Grimmia*.

These mosses constitute a modest percentage of biomass in many plant communities of Nevada. They are restricted to rock habitat, although *Grimmia occidentalis* is occasionally found on the base of trees near stream sides. *Grimmia* subgenus *Grimmia* generally occurs on dry, exposed rock, but *Grimmia* subgenus *Schistidium*, and *Rhacomitrium* occur on rock that is or has been inundated by water from spring snow melt, or deep within rock crevices that offer protection from exposure to the sun and heat.

Members of the Grimmiaceae display unique composition in three geographical areas in Nevada. These areas are (1) the Mohave Desert in the very southern part of the state, (2) the Great Basin desert and associated mountain ranges, which includes most of the state, and (3) the Sierra Nevada in the very western portion of the state.

The Mohave Desert vegetation is dominated by such vascular plants as *Yucca brevifolia* (Joshua tree) and *Larrea tridentata* (creosote bush). In this desert, *Grimmia orbicularis, G. wrightii, G. anodon,* and *G. affinis* are the dominant and practically the only mosses, sometimes codominating the cryptogamic flora with *Tortula inermis, Crossidium abberans, C. griseum,* and the hepatic *Targonia heterophylla*. *Grimmia affinis*, originally described as autoicous, is dioicous in Nevada. This agrees with Flowers (1973).

Mesic habitats in this southern desert are found in unusual abundance in the deep canyons of the Spring Mountains just west of Las Vegas. Here, *Grimmia ovalis, G. pulvinata, G. stricta,* and *G. atricha* grow, along with other common mosses such as *Anacolia menziesii, Brachythecium collinum, Encalypta intermedia* (i.e. *Encalypta intermedia*), and *Orthotrichum cupulatum*. *Grimmia ovalis* forms unusually long stems in this area, up to 6 cm in length.

G. pulvinata, G. atricha, and *G. stricta* occur throughout the Pacific Northwest and might, therefore, be expected to occur in more northerly portions of Nevada. However, the only Nevada collections come from the southern part of the state. *Grimmia atricha* is reported from the Spring Mountains by a collection of Dr. H. Mozingo, University of Nevada, Reno. This represents possibly the most southern distribution for this species. Many endemic and relictual vascular plants occur on this range and this moss could be a holdover from Pleistocene vegetation.

The Great Basin Desert vegetation is dominated by *Artemisia tridentata* (big sage), *Pinus monophylla* (single leaf pinyon pine), and *Juniperus osteosperma* (Utah juniper). Cryptogamically, it is dominated by *Grimmia tenerrima, G. anodon,* and *G. calyptrata*. These three mosses commonly grow together at practically all elevations. *Grimmia calyptrata* inhabits predominantly the northwestern exposures, and *G. tenerrima* and *G. anodon* assume the somewhat more protected northeast exposures. As *G. tenerrima* is dioicous, the male and female plants appear as separate entities due to differences in the lengths of the hairpoints. The male plant, with very short hairpoints, is often confused with *G. anodon. G. anodon*, however, is autoicous, thereby making the two easily separable.

---

[1] P.O. Box 13494, Reno, Nevada 89507.

Grimmia anodon has the most widespread distribution of probably any plant species in Nevada. The plants in southern Nevada have a much greener appearance, shorter hairpoints, and more erect stems than the same species from the north. *Grimmia calyptrata*, although abundant in northern Nevada, is not found in southern Nevada. It is, apparently, ecologically replaced by *G. orbicularis* in the south. They both inhabit very exposed rock and superficially resemble each other with regard to long hairpoints on the leaves and the large rounded clumps they both form (resembling small hedgehogs).

Table 1. A list of the Grimmiaceae in Nevada. Nomenclature for *Grimmia* subgenus Grimmia and *Rhacomitrium* generally follows Lawton (1971). Nomenclature for the specific epithet in *Grimmia* subgenus Schistidium is based on Deguchi (1979).

Grimmia (subgenus Grimmia)
- *affinis* Hornsch.
- *anodon* B.S.G.
- *calyptrata* Hook. ex Drumm.
- *laevigata* Brid.
- *montana* B.S.G.
- *orbicularis* Bruch.
- *ovalis* (Hedw.) Lindb.
- *plagiopodia* Hedw.
- *poecilostoma* Card. & Seb.
- *pulvinata* (Hedw.) Small
- *tenerrima* Ren. & Card. (SY = *G. alpestris* [Web. & Mohr] Nees)
- *torquata* Hornsch. var. *torquata*
- *trichophylla* Grev.
- *wrightii* (Sull.) Aust.

Grimmia (subgenus Schistidium)
- *alpicola* Hedw. (SY = *G. agassizii* (Sull. & Lesq. ex Sull.) Jaeg. & Sauerb. See Bremer (1980) and Deguchi (1979 and 1979a) for nomenclature of this entity.)
- *alpicola* var. *latifolia* (Zett.) Moll.
- *ambigua* Sull.
- *apocarpa* Hedw.
- *atricha* C. Muell & Kindberg ex Macoun & Kindberg
- *conferta* Funck
- *flaccida* (DeNot.) Lindb.
- *occidentalis* Lawton
- *pacifica* Lawton
- *rivularis* Brid. (SY = G. alpicola var. rivularis [Brid.] Wahlenb.)
- *stricta* Turn.

Rhacomitrium
- *heterostichum* (Hedw.) Brid. var. *heterostichum* (verified by Lawton, 1981)

On the granitic boulders that follow Salmon Falls Creek in Elko County of northeastern Nevada, *G. poecilostoma* occurs, far north of its otherwise reported range. This moss has supposedly a more southern distribution, including New Mexico, Texas, and Arizona.

In extremely dry situations, such as the flat desert country in westcentral Nevada, *Grimmia anodon* is almost the only existing moss, inhabiting mostly low lying, flat rock. Mosses commonly occurring with the *Grimmia* species of this part of the Great Basin include *Brachythecium collinum, Dicranowesia crispula, Encalypta intermedia, Orthotrichum cupulatum, O. jamesianum, O. laevigatum* f. *macounii, Pseudoleskeella tectorum, Pterygoneurum ovatum, P. subsessile, Timmia megapolitana, Tortula papillosissima*, and *T. ruralis*.

Following spring snow melt runoff in the high mountains of the Great Basin, rocks are inhabited by a few members of *Grimmia* subgenus *Schistidium*. These species include *G. occidentalis, G. rivulare, G. alpicola*, and *G. pacifica*. These mostly occur by themselves, but may occur with such mosses as *Lescuraea incurvata* or *Orthotrichum rivulare*. These mosses nearly always inhabit montane to alpine environments. However, *G. occidentalis*, along with *Orthotrichum rivulare*, was observed to occur in the pinyon-juniper woodlands of the Virginia Range of westcentral Nevada.

Grimmia pacifica, collected in the Santa Rosa Range of northcentral Nevada, is a very interesting plant. The spores measure up to 30 μm in diameter, and the upper portions of the leaves are keeled with some of the lower leaf margins slightly recurved. This lends some doubt as to its identification, but Lawton (1980) indicates that this species is rarely collected and it may be another variable species in the Grimmiaceae. Personal observation of this specimen plus other specimens from the Pacific Northwest have suggested that this entity may be nothing more than an ecotype of *G. apocarpa*.

The most successful member of *Schistidium* in Nevada is *G. flaccida*. It is the only Schistidium that inhabits extremely dry rock outcrops in this state. It is mostly not found on extreme exposures (southwest faces) but is more commonly found within protected rock crevices on northern exposures. In Nevada, it is interesting to note that the most common *Grimmia*, *G. anodon*, and the most common Schistidium, *G. flaccida*, are the only two members of the Grimmiaceae in Nevada that completely lack a peristome. The latter species is common in northern Nevada even though records appear to the contrary.

In the northeastern portion of Nevada, the Great Basin has a greater diversity of dry rock *Grimmia*. Aside from the three dominants previously listed, *G. ovalis*, *G. poecilostoma*, *G. apocarpa*, and *G. flaccida* occur in greater abundance. *Grimmia ambigua* and *G. conferta*, also occur in this area, but more commonly inhabit deep crevices or shady north faces of rocks and boulders. *Grimmia conferta*, in its habitat and general appearance, appears to be a link that connects the subgenera Schistidium and Grimmia. In Wyoming, Idaho, and parts of northeastern Nevada, this moss forms small rounded clumps on exposed rock surfaces, a habit typical of members of *Grimmia* subgenus Grimmia.

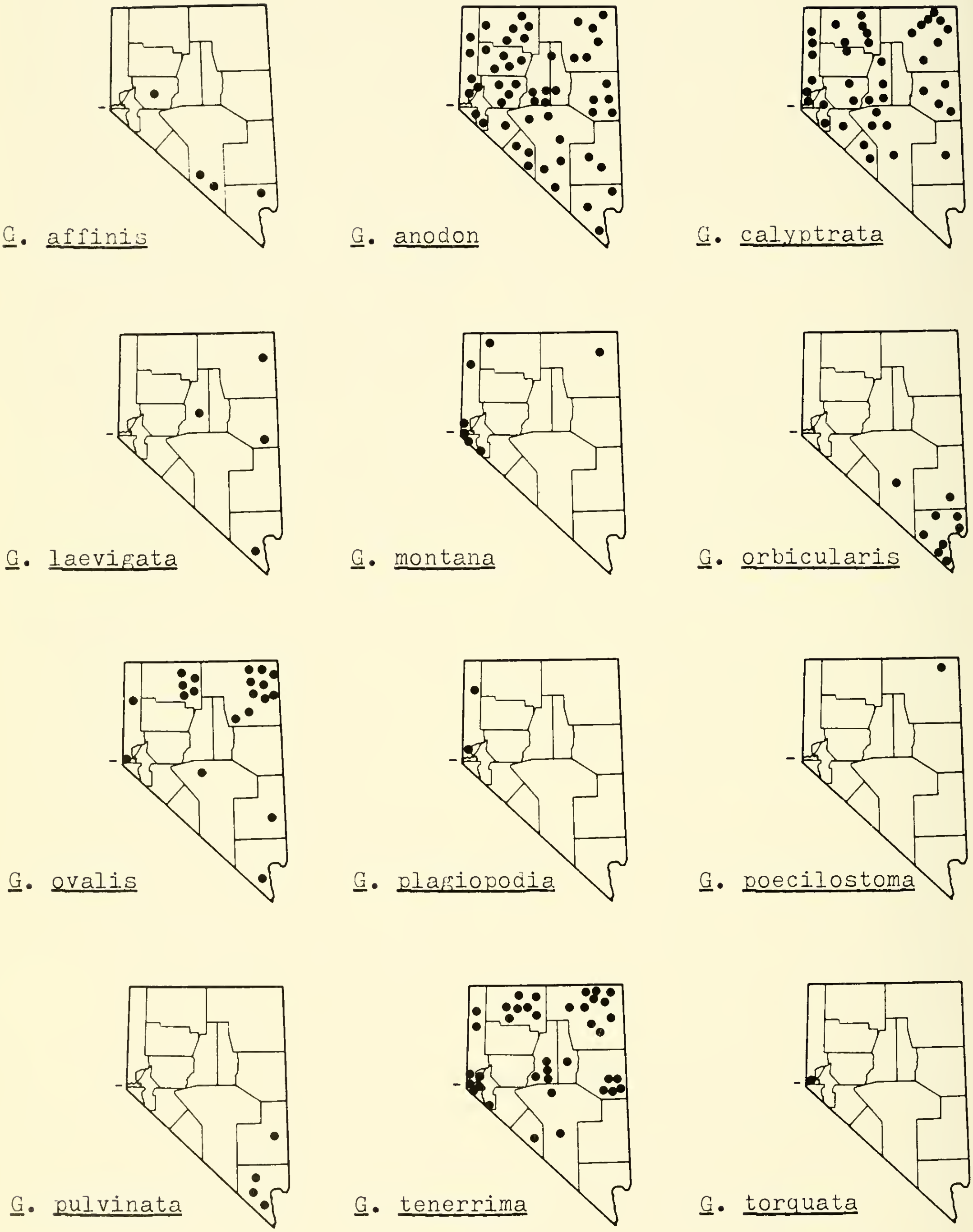
The Jarbidge, Ruby, East Humboldt, and Snake mountains are located in the northeastern portion of Nevada. It is in these mountains that many vascular plants from the Rocky Mountains and Pacific Northwest make their only appearance in Nevada. These vascular plants include *Abies lasiocarpa, Silene acaulis, Saxifraga caespitosa, Arctostaphylos uva-ursi, Primula parryi, Selaginella selaginoides*, and *Astragalus aboriginum*. Along the same lines, the montane environments in northeastern Nevada provide habitat for *G. alpicola, G. ambigua, G. conferta, G. rivulare*, and *G. alpicola* var. *latifolia*.

The Sierra Nevada, characterized by the Jeffery pine, lodgepole pine, red fir, and whitebark pine forests, is dominated, with regard to mosses, by *Grimmia tenerrima* and *G. montana*. *Grimmia trichophylla* and *G. torquata* are present and appear to be unique, in Nevada, to this area. Of particular interest in the Sierra Nevada is the absence of *G. anodon*. This is unusual because this moss is the most widespread in the state, occurring in all counties and elevations from below 300 m in the south to over 4000 m on top of Mount Moriah in east central Nevada. One specimen of *G. anodon* was found in the Sierra Nevada just west of Carson City on Snow Valley Peak. It is a very atypical specimen in that its seta ranges from straight to arcuate and the calyptra is large and cucullate, as well as typically small and mitrate. Substrate does not appear to have a role in the exclusion of *G. anodon* from the Sierra Nevada. The granodiorites of the Fox, Sellinite, Granite, and Wassuk ranges of western Nevada are inhabited frequently by *G. anodon*. These granodiorites are similar and genetically related to the granodiorite of the Sierra Nevada Batholith (Hibbard 1982). Snow pack or summer aridity of the Sierra doesn't play a role either: *G. anodon* occurs in high montane habitats throughout the Great Basin, as well as throughout the desert areas of the state.

Rock inundated by spring snow melt runoff in the Sierra Nevada provides habitat for both *Grimmia occidentalis* and *G. apocarpa*. These are fairly common mosses throughout the entirety of the high montane habitats in the southern Sierra. Also present is *Rhacomitrium heterostichum* var. *heterostichum*, but very rarely in the Nevada portion of the Sierra Nevada. These wet rock mosses occur by themselves and dry rock *Grimmia* occur commonly with *Dicranoweisia crispula, Enclypta vulgaris* var. *vulgaris, Homalothecium nevadense, Orthotrichum laevigatum*, f. *macounii, O. praemorsum, O. pylaissi, Tortula papillosissima*, and *T. princeps*.

Acknowledgments

This study was funded in part by a grant from Sigma Xi. I am especially grateful to Dr. Elva Lawton for determination and verification of many specimens. I thank Dr. Richard Rust and Dr. H. Mozingo, University of Nevada, for providing much of the field transportation throughout Nevada. Additionally, I thank Dr. Dale Vitt, University of Alberta, for identifying the associated species, namely *Orthotrichum*.



G. affinis

G. anodon

G. calyptrata

G. laevigata

G. montana

G. orbicularis

G. ovalis

G. plagiopodia

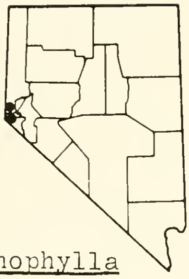
G. poecilostoma

G. pulvinata

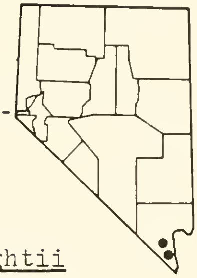
G. tenerrima

G. torquata

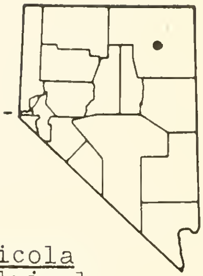
Fig. 1. Distribution of the Grimmiaceae of Nevada. Representative specimens are deposited at the University of Washington, Seattle (WTU). Distribution data come from collections and observations of the author, collections of Dr. H. Mozingo, the University of Nevada, and literature citations given by Lawton (1958). *Grimmia torquata* was not found during the course of this study so the location given by Lawton (1958) is used.



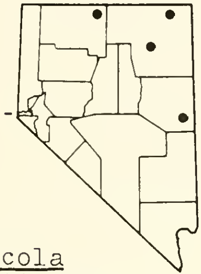
G. trichophylla



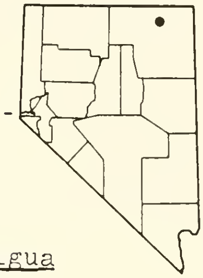
G. wrightii



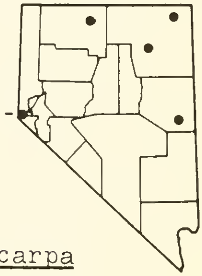
G. alpicola var. *alpicola*



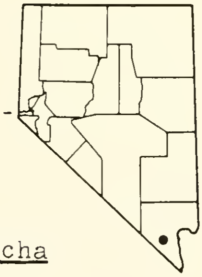
G. alpicola var. *latifolia*



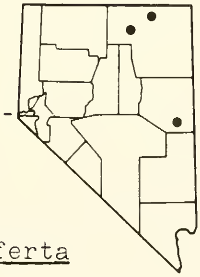
G. ambigua



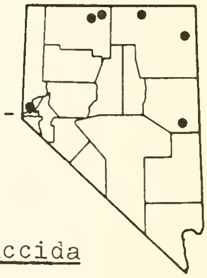
G. apocarpa



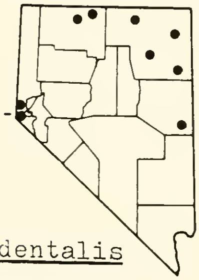
G. atricha



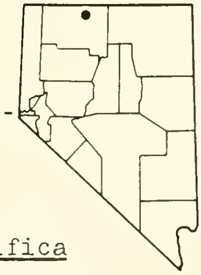
G. conferta



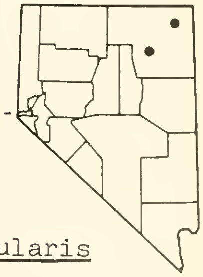
G. flaccida



G. occidentalis

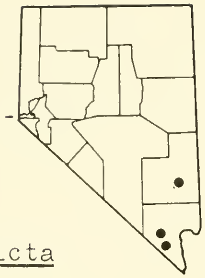


G. pacifica



G. rivularis

Fig. 1 continued.



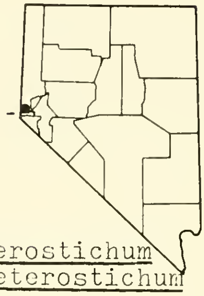


Fig. 1 continued.

LITERATURE CITED

BREMER, B. 1980. Proposal to reject the names *Grimmia alpicola* Sw. ex Hedw. and *Schistidium alpicola* (Sw. ex Hedw.) Limpr. (Grimmiaceae). Taxon 29:337–339.

DEGUCHI, H. 1979. A revision of the genera *Grimmia*, *Schistidium*, and *Coscinodon* (Musci) of Japan. J. Sci. Hiroshima University, Series B, Div. 2, 16:121–250.

______. 1979a. Les veritables caracteres de *Schistidium alpicolum* (Sw. ex Hedw.) Limpr. et son nouveau synonyme *Schistidium agassizii* Sull. et Lesq. Rev. Bryol. Lichenol. 45(4):425–435.

FLOWERS, S. 1973. Mosses of Utah and the West. Brigham Young University Press, Provo, Utah.

HIBBARD, M. 1982. Personal communication. University of Nevada, Reno.

LAWTON, E. 1958. Mosses of Nevada. Bryologist 61:314–340.

______. 1971. Moss Flora of the Pacific Northwest. Hattori Botanical Laboratory. Nichinan.

______. 1980. Personal communication. University of Washington, Seattle.

INSULAR BIOGEOGRAPHY OF MAMMALS IN THE GREAT SALT LAKE

Michael A. Bowers[1]

Abstract.— The distribution of 21 species of nonvolant mammals among nine islands in the Great Salt Lake was analyzed for biogeographic patterns. The number of species inhabiting an island is closely correlated with island area. That the slope of the regression line describing this relationship (z or b) is relatively shallow compared to (1) totally isolated island systems or (2) island systems where an equilibrium between rates of colonization and extinction have been attained suggests that isolation plays little role in accounting for the variation in mammalian species diversity among islands. Stepwise multiple regression confirms this, while demonstrating that area alone accounts for 88 percent of the variation in species diversity among islands. However, endemic subspecies comprise a significant proportion of the insular mammalian fauna, suggesting that isolation for small mammals restricted to certain habitats may be substantial. A general scenario of the processes determining insular mammalian diversity and endemism is discussed for the Great Salt Lake, where the dynamic lake level creates a potential for different biogeographic processes over time.

Analysis of the distribution of nonvolant mammals among oceanic (Carlquist 1965, Wright 1981), landbridge (Hope 1973, Southern 1964, Bloeker 1967, Wright 1981), and montane (Brown 1971, 1978) islands has played a significant role in the development and testing of contemporary biogeographic theory (reviews by Brown 1978, Wright 1981). However, most emphasis in the current biogeographic literature focuses on the distribution of reptiles and birds (Carlquist 1965, Simberloff 1974, Wright 1981). Although the conspicuousness of these vertebrates facilitate the quantification of species in insular habitats, the poor dispersal abilities of nonvolant mammals (Carlquist 1965, Brown 1971, 1978, Wright 1981) make them particularly interesting subjects for biogeographic analysis.

Isolated habitats in the Intermountain Region of western North America have provided several good tests of biogeographic theory (review by Harper and Reveal 1978). Rigorous interpretation of such patterns have been possible because the paleoclimatic history of the region is well understood (Hubbs and Miller 1948, Martin and Mehringer 1965, Wells and Berger 1967, Wells and Jorgensen 1964).

This paper discusses the distribution of nonvolant mammals among islands in the Great Salt Lake in relation to the theory of insular biogeography. Special emphasis relates distributional patterns to the process of extinction and dispersal, which appear to reflect historical events rather than equilibrial processes.

Methods

The distribution of nonvolant mammalian species among nine islands in the Great Salt Lake was compiled from published literature (Stansbury 1852, Fremont 1850, Durrant 1936, 1952, Goldman 1939, Marshall 1940). One source (Marshall 1940), which reported the findings of an extensive mammal survey of the Great Salt Lake in the late 1930s, not only documented the distribution of species (and subspecies) by islands, but also characterized in detail the islands proper. Both historical (age of island, number of years connected to the mainland between 1850 and 1940) and physical (area, island height, distance to mainland) features were included in the general description of each island. Marshall (1940) and Durrant (1936, 1952) were particularly interested in the distribution of subspecies restricted to certain islands in the Great Salt Lake. Although both of these authors invoked historical explanations to account for the distribution of mammals in general and endemic subspecies in particular, little emphasis was given to the quantitative analysis of determinants affecting the dispersion of species and subspecies over the nine islands. In the present paper I reanalyze the baseline data reported by Marshall (1940) in a quantitative manner and interpret the results in light of recent contributions to the general theory of biogeography. The general taxonomy follows Goldman (1939) and Durrant (1952). Introduced mammalian species and all chiropterans were excluded from the analysis. For a more detailed account of the islands, see Marshall (1940).

---

[1] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721.

RESULTS AND DISCUSSION

As of 1938, 21 species of nonvolant mammals were distributed among the nine islands (Table 1) of the Great Salt Lake. Moreover, nine subspecies were totally restricted in distribution to these islands.

The number of mammalian species (Table 1) inhabiting an island is closely correlated with the area (Table 2) of the island (Fig. 1). When both variables are plotted logarithmically, the data are well described ($r=.74$) by a straight line with a slope (z) of .19. Traditionally, biogeographers have expressed this relationship as $S=CA^z$, where S is the number of species inhabiting an island and A is the insular area. The value of the constant (C) and slope (z) have been shown to be dependent on the specific taxon and group of islands under consideration (MacArthur and Wilson 1967, Preston 1962, Wright 1981). Widespread use of the power function has proved beneficial in that it facilitates the comparison of slopes and, in an *a priori* sense, biogeographical processes that are impacting insular systems (reviews by Brown 1978, Wright 1981).

TABLE 1. Distribution of subspecies, by island, for mammals in the Great Salt Lake. Taxonomy from Goldman (1939) and Durrant (1952).

	Dolphin	Gunnison	Bird (Hat)	Sand bar	Carrington	Badger	Stansbury	Antelope	Fremont
Dipodomys microps russeolus°	X								
Dipodomys microps alfredi°		X							
Dipodomys microps subtenuis					X	X	X		
Dipodomys ordii marshalli			X		X	X	X		
Dipodomys ordii cineraceus°	X								
Dipodomys ordii utahensis								X	
Perognathus parvus plerus°					X		X		
Thomomys bottae minimus°							X		
Thomomys bottae nesophilus°								X	
Eutamias minimus pictus							X		
Spermophilus townsendii mollis	X						X	X	X
Erethizon dorsatum epixanthum	X						X		
Peromyscus crinitus pergracilis							X		
Peromyscus maniculatus sonoriensis	X		X	X	X	X	X	X	
Peromyscus maniculatus gunnisoni°		X							
Peromyscus maniculatus inclarus°									X
Reithrodontomys megalotis ravus							X		
Neotoma lepida marshalli°					X	X	X		
Neotoma lepida lepida	X							X	
Onychomys leucogaster utahensis							X		
Sylvilagus nuttalli grangeri					X	X	X	X	
Lepus californicus deserticola							X	X	X
Odocoileus hemionus hemionus							X	X	
Antiocapra americana americana								X	
Lynx rufus pallescens							X	X	
Mustela frenata nevadensis								X	
Taxidea taxus taxus							X		
Mephitis mephitis major							X	X	
Canis latrans lestes	X		X		X	X	X	X	
Total species	7	2	3	1	7	6	19	13	3

°Subspecies not found on the mainland.

The z-value (.19) for nonvolant mammals inhabiting islands in the Great Salt Lake is slightly lower than insular biotas where an equilibrium between rates of colonization and extinction have been attained (.20–.35, MacArthur and Wilson 1967). However, the z-value for insular habitats in the present analysis is larger than those commonly reported for continental situations (.12–.17, MacArthur and Wilson 1967) and is comparable to two decimal places the value reported in a recent vegetational analysis of a pinyon-juniper ecosystem where nested quadrants were used as islands (Harner and Harper 1976).

The slight deviation from predicted z-values for continental and equilibrial insular systems can be elucidated through stepwise multiple regression analysis of island characteristics (Table 2) on the number of resident mammal species (Table 1). Similar multivariate techniques have been extremely powerful when investigating the significance of interdependent island characteristics (Table 3) on the variation in insular species diversity (Brown 1971, 1978, Harper et al. 1978).

That (a) approximately 88 percent of the variation in insular mammalian diversity can be accounted for by island area (Table 4), and (b) there appears to be little impoverishment of species number resulting from isolation by distance to the mainland (Table 4) suggest that colonization rates are high and that there is little effect of insular isolation on species richness. These results appear to be consistent with those of others (Johnson 1975, Brown 1978) studying boreal birds in intermountain habitats where avian diversity is attributable primarily to the diversity of available habitats and not area per se. Specifically, the overwhelming dominance of area in the multiple regression analysis (Table 4) is in all probability an illusion. Wyckeroff (1973) and Harner and Harper (1976) have demonstrated that both environmental favorability and heterogeneity exert a strong influence on the number of vascular plant species per unit area. Because area alone subsumes all these variables, it by itself accounts for several variables that *a priori* could account for a significant amount of the variation in mammalian species diversity. Unfortunately, data on environmental favorability and heterogeneity are not available for the islands in the Great Salt Lake. Quantification and analysis of habitat diversity patterns of the islands would be a strong test of the effect of area, per se, on variation in the number of mammalian species in this system of islands.

On the islands of the Great Salt Lake, recurrent colonization appears to be much more important than local extinction. This contention can be examined in more detail by looking at ecological attributes of the 21 species that are distributed among the nine islands. In particular, the documentation of characteristics that might increase the probability of local extinction could produce a finer degree of resolution than examining entire island compositions.

TABLE 2. Historical and physical data for the nine islands in the Great Salt Lake. Data adapted from Marshall (1940).

Island	Area (hectares^2)	Distance[1] (km)	Height[2] (m)	Corridor[3] height (m)	Years[4] connected	Age[5] (years)
Dolphin	20.7	5.67	18.5	.77	18	20,000
Gunnison	67.4	24.30	46.2	−1.23	0	20,000
Bird (Hat)	9.1	32.40	12.3	.31	12	20,000
Sand bar	.2	37.26	.6	.31	7	6
Carrington	730.2	32.40	123.0	.31	12	20,000
Badger	2.5	35.64	3.1	.31	13	50
Stansbury	7,977.3	19.44	769.2	3.01	76	70,000
Antelope	10,766.9	5.27	737.8	.92	19	70,000
Fremont	1,216.9	24.30	244.9	.46	2	70,000

[1] Distance (km) from island to the nearest mainland area.

[2] Maximum height (m) of an island relative to zero (= 1291.3m) on the Saltair gage.

[3] Height (m) of connecting bar on the Saltair gage.

[4] Years an island was connected to the mainland between 1850 and 1938.

[5] Probable age of an island (see Marshall 1940).

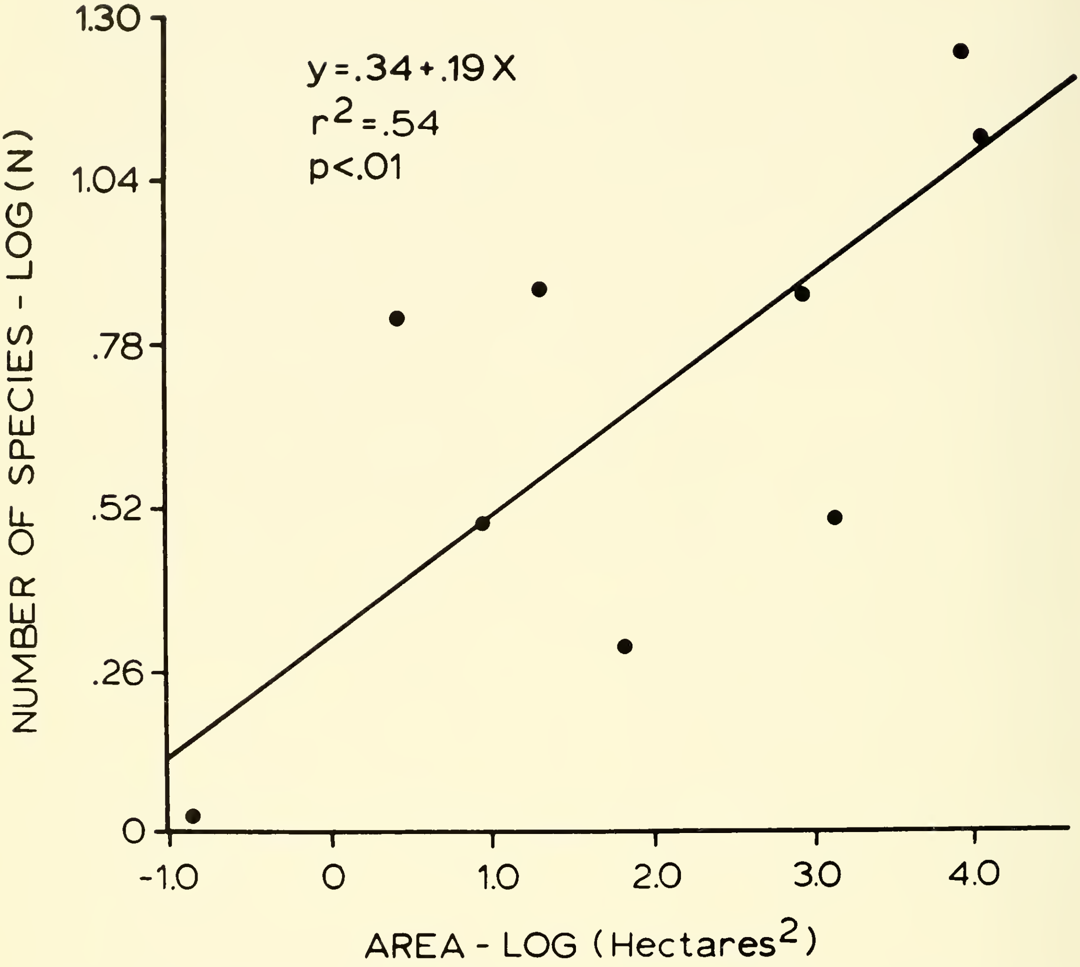


Fig. 1. The relationship between insular area and the number of nonvolent mammal species for the nine islands in the Great Salt Lake. The equation for the fitted regression and the amount of variance in mammalian species diversity accounted for by area (r^2) are indicated.

The probability of a species becoming extinct appears to be directly dependent on local population size (MacArthur and Wilson 1963, 1967). In addition to island size, three ecological variables appear to be particularly important in determining insular population size. These variables—body size, trophic status, and degree of habitat specialization—affect the distribution of mammalian species among the Great Salt Lake islands in the manner we would expect from considerations of their effects on population size: small mammals are found on more islands than large ones (Fig. 2), herbivores are better represented than granivores, insectivores, or carnivores, and species that can live only in restricted habitats inhabit fewer islands than species with the same trophic affinities but who are habitat generalists. Figure 2 shows the relationship between the number of islands inhabited by a particular species and the logarithm of body weight. Generally these variables do not covary to any significant extent ($r = -.28$). However, within the herbivore guild (Fig. 2) the number of islands inhabited by a species is negatively ($P < .04$) correlated with the logarithm of body weight ($y = .64 - .09x$, $r = -.65$, $df = 7$). Within this guild, the species of largest body size occur only on the larger islands (Tables 1 and 2),

Table 3. Correlation coefficients (r) between variables for the nine islands in the Great Salt Lake. Matrix is computed with untransformed data. Note that the number of total species and endemic subspecies are not always closely correlated with the same variables.

	Area	Distance	Height	Corridor height	Years connected	Age	Number of species
Area	—						
Distance	-.593	—					
Height	.970	-.547	—				
Corridor height	.630	-.279	.677	—			
Years connected	.610	-.272	.705	.941	—		
Age	.772	-.583	.859	.402	.466	—	
Number of species	.938	-.605	.924	.789	.766	.676	—
Number of endemic subspecies	.240	.013	.395	.663	.820	.663	.467

suggesting the importance of matching body size (and, hence, population size) with suitable habitat patch size, which appears to covary with island area. In fact, those species of both large and small body size that occur on only a few islands usually are found only on large islands (Tables 1 and 2). Thus, it appears that, for mammals on islands in the Great Salt Lake, insular area not only affects the number of species but also can be used to predict some ecological attributes of the denizens.

The preceding analyses suggest that isolation of insular habitats in the Great Salt Lake is relatively unimportant in determining mammalian diversity. However, the fact that such a high proportion of the island faunas are composed of endemic subspecies strongly suggests that isolation has been a prominent factor, at least in the past, in the evolution of these insular biotas. The determinants promoting endemism can be examined by using the proportion of subspecies endemic on each island (Table 1) as the dependent variable and island characteristics as the independent variables (Table 2) in a stepwise multiple regression. The results of this analysis (Table 5) show that two variables (height of the corridor connecting the various islands with the mainland and number of years between 1850 and 1938 that an island was connected to the mainland) explain 76 percent of the variation in the proportion of insular subspecies that are endemic. Obviously, the degree of isolation as reflected by corridor height and years connected to the mainland are imminently important in producing and maintaining endemic subspecies in insular mammalian faunas. It should be noted that in this particular analysis subspecies are considered endemic if the corresponding mainland species are of different subspecies. Consequently, endemic subspecies can and do occur on several islands.

In the analysis of species distributed among islands, isolation played little role in accounting for the patterns. In contrast, the occurrence of endemic subspecies is highly correlated with the degree of isolation. These differences can be reconciled by examining ecological attributes of the endemic subspecies. That all endemic subspecies are herbivores, granivores, or omnivores and are relatively small (<300g) when compared with the other species that are distributed among the nine islands suggests that population size may effect the rate of local genotypic differentiation from mainland populations. Specifically, the data suggest that species capable of maintaining large insular populations per

Table 4. Summary of stepwise multiple regression of the influence of island characteristics on the number of mammalian species on islands in the Great Salt Lake.

Variable[a]	Order entered in equation	Contribution to R^2	F-value	Significance level
Area	1	0.882	52.16	.0001
Corridor height	2	0.065	7.36	.035
Distance	3	0.008	.96	.373

[a] Data from Table 2 (untransformed).

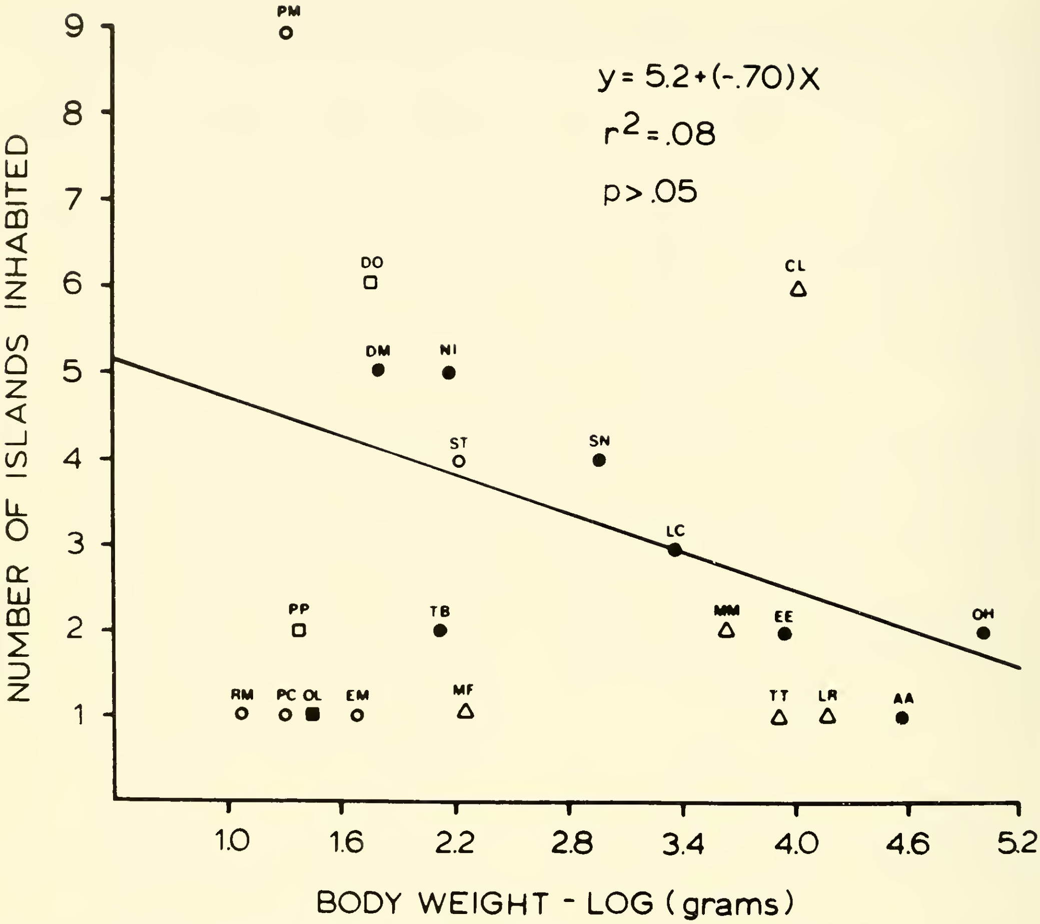


Fig. 2. Frequency of occurrence of species of nonvolent mammals on the nine islands in the Great Salt Lake plotted against body weight; solid circles represent herbivores, hollow circles represent omnivores, hollow squares represent granivores, hollow triangles represent carnivores, and solid squares represent insectivores. Letters adjacent to each point refer to species names that can be identified by reference to Table 1.

unit area are more likely to show substantial differentiation from the mainland populations than species with smaller populations.

Two interdependent factors may account for these differences. First, as a consequence of larger body size, and thus mobility, more colonists of large-bodied species probably disperse to islands than smaller species. Thus, the amount of gene flow from mainland to island populations would be relative to body size: e.g., because of intrinsic differences in dispersal ability insular populations of large species would be expected to have gene frequencies closer to those mainland populations when compared to smaller species. Second, given that a single colonist did disperse to an island from the mainland, the incorporation and ultimate fixation of its genes into the genepool of the population would be a negative function of population size. Specifically, the larger the population the greater the likelihood that a single colonist's contribution of novel genes will be swamped: e.g., the infusion of new genetic material from one act of colonization will be much greater in a population of 10 individuals when compared to a population of 100.

Although the analyses presented in this present paper generally suggest that isolation has not been important in limiting the distribution of nonvolant mammals among the islands in the Great Salt Lake, a caveat should be interjected. Specifically, the survey by Marshall (1940) was conducted when the lake

TABLE 5. Summary of stepwise multiple regression of the influence of island characteristics on the proportion of subspecies that are endemic for the nine islands in the Great Salt Lake.

Variable[a]	Order entered in equation	Contribution to R^2	F-value	Significance level
Corridor height	1	.16	1.32	.287
Years connected	2	.60	14.64	.009
Age	3	.07	2.08	.208

[a] Data from Table 2 (untransformed).

level was near a 100-year minimum. Colonizations by mammals just prior to the survey could effectively obscure patterns of local extinctions, thereby downplaying the role of isolation. Since that time, the lake level has remained relatively high.

A strong test of the result presented here would be to re-census the islands while testing for the effects of isolation. Not only would this yield valuable biogeographical information, but it would serve as one of the few instances where island relaxation rates (Diamond 1972, 1975) could be precisely quantified because the exact year of isolation by island is known through the detailed documentation of the lake level (U.S. Weather Bureau).

GENERAL DISCUSSION

The distribution of nonvolant mammals among nine islands in the Great Salt Lake appears to reflect the effect of recurrent colonizations rather than the equilibrial processes of extinction and immigration. Consequently, islands appear to be "saturated" with species and the distribution of species among islands is probably determined by the distribution of amicable habitats that are extensive enough to support populations of the colonists. However, isolation of insular habitats does appear to be important for some species of small body size. This is supported by a high degree of endemism for these species.

The failure of the equilibrium theory of biogeography (MacArthur and Wilson 1963, 1967) to account for the distribution of mammals among insular habitats studied here supports a general trend that contrasts intermountain insular habitats with oceanic island systems. Specifically, the distribution of birds (Johnson 1975, Behle 1978), mammals (Brown 1971, 1978), fish (Smith 1978) and even plants (Harper et al. 1978) among insular habitats in western North America rarely conform to equilibrial predictions. In contrast, the biotas of oceanic islands often exhibit equilibrial distributions (Simberloff 1974, Wright 1981). This difference is correlated with contrasting paleoclimatic and geological processes impacting the two types of insular systems. Over the last million years extensive climatic and geological changes have drastically changed and, for islands in the Great Salt Lake, are still changing the landscape of western North America (see earlier citations of Hubbs, Martin, Wells). Oceanic systems, however, have a long history of isolation and relative environmental stability (MacArthur and Wilson 1967, Simberloff 1974). It is possible that these differences in the underlying environmental patterns (both past and present) account for the contrasting biogeographic tendencies. As pointed out by Brown (1978), these dynamic environmental factors should differentially affect species with contrasting vagilities. Because mammals in general are relatively poor dispersers across unsuitable habitats (Brown 1971, 1978) and aquatic barriers (Carlquist 1965), it is interesting to speculate what biogeographic model the Great Salt Lake islands would conform to if the islands were isolated for long periods of time. In all probability the maintenance of a high lake level would create a system analogous to that of boreal mammals on mountain tops (Brown 1971, 1978), where extinctions are dependent on insular size and colonizations are rare. Such processes may currently be in effect with the higher lake level.

ACKNOWLEDGMENTS

Initial interest in the quantification of mammals distributed among islands in the Great Salt Lake was generated through discussions with T. C. Gibson and J. H. Brown.

The present analyses would have been impossible without the pioneering work of natural historians and systematists who documented in detail the mammalian fauna of the Great Salt Lake area. To all the above I am grateful.

LITERATURE CITED

BEHLE, W. H. 1978. Avian biogeography of the Great Basin and Intermountain Region. Great Basin Nat. Mem. No. 2:55–88.

BLOEKER, J. C. VON, JR. 1967. Land mammals of the southern California islands. R. N. Philbrick, ed., Proceedings of the Symposium on the Biology of the California Channel Islands. Santa Barbara Botanic Garden. Santa Barbara, California, USA.

BROWN, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist 105:467–478.

_____. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Nat. Mem. No. 2:209–227.

CARLQUIST, S. 1965. Island life. Natural History, New York, New York.

DIAMOND, J. M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. Proc. U.S. Nat. Acad. Sci. 69:3199–3203.

_____. 1975. Assembly of species communities. Pages 342–444 *in* M. L. Cody and J. M. Diamond, eds., Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA and London, England.

DURRANT, S. D. 1936. A new gopher from Antelope Island, Great Salt Lake, Utah. J. Mammal. 20:351–357.

_____. 1952. Mammals of Utah: taxonomy and distribution. Univ. Kansas Publ. Lawrence, Kansas, USA.

FREMONT, J. C. 1850. The exploring expedition into the Rocky Mountains, Oregon California. Derby and Co., Buffalo, New York, USA.

GOLDMAN, E. A. 1939. Nine new mammals from islands in the Great Salt Lake, Utah. J. Mammal. 20:351–357.

HARNER, R. F., AND K. T. HARPER. 1976. The role of area, heterogeneity, and favorability in plant species diversity of pinyon-junior ecosystems. Ecology 57:1254–1263.

HARPER, K. T., D. C. FREEMAN, W. K. OSTLER, AND L. G. KLIKOFF. 1978. The flora of Great Basin mountain ranges: diversity, sources, and dispersal ecology. Great Basin Nat. Mem. No. 2:81–103.

HARPER, K. T., AND J. L. REVEAL, eds. 1978. Intermountain biogeography: a symposium. Great Basin Nat. Mem. No. 2:1–268.

HOPE, J. H. 1973. Mammals of the Bass Straight Islands. Proc. Roy. Soc. Victoria 85:163–195.

HUBBS, C. L., AND R. R. MILLER. 1948. Correlation between fish distribution and hydrographic history in the desert basins of western United States. Pages 17–166 *in* The Great Basin, with emphasis on glacial and postglacial times. Bulletin of the Univ. of Utah 38:1–191.

JOHNSON, N. K. 1975. Controls of numbers of bird species on montane islands in the Great Basin. Evolution 29:545–557.

MACARTHUR, R. H., AND E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373–387.

_____. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey.

MARSHALL, W. H. 1940. A survey of the mammals of the islands in Great Salt Lake, Utah. J. Mammal. 21:144–159.

MARTIN, P. S., AND P. J. MEHRINGER. 1965. Pleistocene pollen analysis and biogeography of the Southwest. Pages 435–451 *in* H. E. Wright and D. G. Frey, eds., The quarternary of the United States. Princeton Univ. Press, Princeton, New Jersey, USA.

PRESTON, F. W. 1962. The canonical distribution of commonness and rarity: Part I. Ecology 43:185–215.

SIMBERLOFF, D. S. 1974. Equilibrium theory of island biogeography and ecology. Ann. Rev. Ecol. Syst. 5:161–182.

SMITH, G. R. 1978. Biogeography of intermountain fishes. Great Basin Nat. Mem. No. 2:17–42.

SOUTHERN, H. N. 1964. The handbook of British mammals. Blackwell Scientific, Oxford, England.

STANSBURY, H. 1852. Exploration and survey of the Valley of the Great Salt Lake of Utah. Lippincott, Gromlee and Co., Philadelphia, Pennsylvania, USA.

U.S. WEATHER BUREAU. 1979. Climatological data (series by states).

WELLS, P. V., AND R. BERGER. 1967. Late Pleistocene history of coniferous woodland in the Mojave Desert. Science 155:1640–1647.

WELLS, P. V., AND C. D. JORGENSEN. 1964. Pleistocene woodrat middens and climatic change in the Mojave Desert: a record of juniper woodlands. Science 143:1171–1173.

WRIGHT, S. J. 1981. Intra-archipelago vertebrate distributions: the slope of the species-area relation. American Nat. 118:726–748.

WYCKOFF, J. W. 1973. The effect of soil texture on species diversity in an arid grassland of the eastern Great Basin. Great Basin Nat. 33:163–168.

DORSAL HAIR LENGTH AND COAT COLOR IN ABERT'S SQUIRREL (*SCIURUS ABERTI*)

Denis C. Hancock, Jr.[1], and Donald J. Nash[1]

ABSTRACT.— *Sciurus aberti,* like many other sciurids including *Sciurus vulgaris* and *Sciurus carolinensis,* shows a coat color polymorphism. Like *Sciurus vulgaris, Sciurus aberti* shows a correlation between coat color phase and dorsal hair length. Both squirrels show an increased frequency of dark morphs in the northern portions of their respective ranges.

A number of sciurids, including *Sciurus aberti* (Ramey and Nash 1976), *Sciurus carolinensis* (Creed and Sharp 1958), and *Sciurus vulgaris* (Voipio 1956) show coat color polymorphisms. The genetics of these polymorphisms seem to involve mutations at the extension locus as with *Sciurus vulgaris,* mutations at the agouti locus as with *Sciurus carolensis,* or mutations at both loci as with *Sciurus aberti* (Searle 1968, Ramey and Nash 1976). For the above three species, field observation and sampling have established that the darker morphs are more common in the northern reaches of their respective ranges or at higher elevations.

Voipio and Hissa (1970) measured hair density and length and related them to pelage color. They found significant differences for hair densities, hair lengths, and hair weights and concluded that hair density was greater for the dark phase of the European Red Squirrel (*Sciurus vulgaris*) than for the light (red) phase.

The present study was designed to examine the relationship between hair length and coat color in Abert's Squirrel (*Sciurus aberti ferreus*). This subspecies occurs in north central Colorado and is the best documented for color polymorphism. It occurs in two main phases: gray and nearly black as well as some intermediate phenotypes (Nash and Seaman 1977). The gray morphs typically show an agouti pigment distribution and the black forms are typically nonagouti. If the squirrels are classified on the basis of pigment distribution, a color range for each group is demonstrated, with those in the nonagouti group tending to be much darker than those in the agouti group.

Dorsal guard hairs and underfurs were measured on 23 specimens of *Sciurus aberti ferreus.* Because Abert's Squirrels were fully protected in Colorado at the time measurements were taken, museum specimens from Colorado State University and the Denver Museum of Natural History were used. A small tuft of hairs was removed at skin level from the middorsal region of each squirrel. Guard hairs were measured three times to the nearest millimeter and averaged, and underfurs were measured as a group to the nearest millimeter. Statistical analyses included mean, standard deviation, and a t-test on the two respective means (agouti and nonagouti squirrels), with the null hypothesis that the two means were the same.

Nonagouti Abert's Squirrel guard hairs ($n = 14$) averaged 23.52 mm in length; Agouti guard hairs ($n = 9$) averaged 20.92 mm. For underhairs, nonagouti ($n = 14$) averaged 15.14 mm and agouti ($n = 9$) averaged 13.00 mm. A T-test was performed on these data and the null hypothesis that the two means were identical was rejected ($p < .001$).

Dark and light pelage appear to be equally effective in heat conservation at lower temperatures (Creed and Sharp 1958), so if response to cold alone were responsible for the maintenance of the polymorphisms discussed here, one could just as likely find a race of lighter than normal squirrels at higher elevations or in northern latitudes, assuming these genes were not deleterious in other ways. However, if genes for longer pelage were associated through linkage or pleiotropism with genes for darker color, the gene or genes could be selected for in colder areas. To confirm this hypothesis, it is necessary to determine the genetic basis for coat color polymorphism more accurately and, having done that, sample the squirrels in their natural habitat while obtaining climatological data for the area of capture. This would determine whether or not there is a significant difference in average climate.

---

[1] Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523.

If there is a link between color phase and hair length in sciurids, it may explain why there do not appear to be many races of lighter than normal squirrels in the northern portions of their ranges.

LITERATURE CITED

Creed, W. A., and W. M. Sharp. 1958. Melanistic gray squirrels in Cameron County, Pennsylvania. J. Mammal. 39:532–537.

Nash, D. J., and R. N. Seaman. 1977. *Sciurus aberti.* Mammalian Species 80:1–5.

Ramey, C. A., and D. J. Nash. 1976. Coat color polymorphism of Abert's squirrel, *Sciurus aberti,* in Colorado. Southwest Nat. 21:209–217.

Searle, A. G. 1968. Comparative genetics of coat colour in mammals. Academic Press, New York. 308 pp.

Voipio, P. 1956. The biological zonation of Finland as reflected in zootaxonomy. Ann. Zool. Soc. Vanamo 18:1–36.

Voipio, P., and R. Hissa. 1970. Correlation with fur density of color polymorphism in *Sciurus vulgaris.* J. Mammal. 51:185–187.

THE RACCOON, *PROCYON LOTOR*, IN WYOMING

E. Blake Hart[1]

Abstract.— Recent distribution maps show raccoon as occupying only the extreme eastern-northeastern portion of Wyoming. However, there is substantial evidence that raccoon are common throughout Wyoming and currently inhabit all the major and many of the minor drainages throughout Wyoming.

The distribution of the raccoon, *Procyon lotor,* has changed rather dramatically in the past few years in Wyoming. Long (1965) recorded that it was present in only five eastern and northeastern counties of Wyoming in 1965. In more recent years, however, evidence has accumulated suggesting that raccoon range is on the increase in the state. Hoffmann, Wright, and Newby (1969) described several localities in adjoining Montana from which raccoon had been taken. Although Hall's (1981) summary showed nearby records in adjacent areas of Idaho, Utah, and Colorado, he also indicated no raccoon localities in central and western Wyoming. Clark, Saab, and Casey (1980) in their review of Wyoming mammal literature likewise presented no new citations on current raccoon distribution. Lotze and Anderson (1979) presented no range extensions.

Dale Weston, a rancher in rural Sage (20 miles south, 2 miles west, Cokeville), Lincoln Co., trapped a raccoon during the winter of 1980–1981. He communicated instances of road kills and had knowledge of trappers who had taken raccoon locally. Upon further inquiry, including written and verbal communication with several fur dealers in western and central Wyoming, we found that the raccoon is presently a common mammal throughout the state and has been for some time, especially the past 5 to 15 years.

Matt Failoni, a fur buyer from Kemmerer, Lincoln Co., stated that he had purchased 51 raccoon pelts around the Kemmerer area in the past five years. James Cook, a fur dealer in Evanston, Uintah Co., had purchased approximately 20 raccoon each year for the past five years.

Recently, Charles Neely, a fur buyer and trapper from Pinedale, Sublette Co., personally trapped 12 raccoon. Due to the paucity of trappers in that area, fewer raccoon have been taken than might otherwise be expected. Beaver trappers occasionally have taken raccoon, but, due to the reduced prices of pelts, fewer beaver traps have been set. Mr. Neely recounted that although few local Pinedale residents raise chickens, every one has called him and complained about raccoon harassment. Mr. Neely further said that his uncle trapped a raccoon locally 30–35 years ago, but in only the past five or so years have numbers of animals increased appreciably. He estimated that extant distribution of raccoon averages one for every three to four miles of creek and river bottom, a total of 30 to 40 raccoons within a 20 mile radius of Pinedale. Mr. Neely suggested that raccoons might have immigrated into the Pinedale area from the south up the Green River drainage system.

Jake Korell, Riverton, Fremont Co., purchased approximately 300 raccoon pelts during the 1981–1982 season and an average of 450 for each of the previous five years, or a total of about 2000 animals. Mr. Korell stated that 46 years ago there were no raccoon in the Riverton area, that they first appeared about 30 years ago. He suggested that contemporary local populations originated both from accidental liberation of pet raccoons by a Missouri family and also from immigration of wild raccoon up local drainage systems.

---

[1] Department of Mathematics and Natural Sciences, Northern State College, Aberdeen, South Dakota 57401.

Mr. Korell also said that the severe winter of 1978–1979 caused significant mortality, that present numbers were down somewhat.

Herman Genz, Rawlins, Carbon Co., trapped and purchased about eight raccoon during the past five years. He caught none in the 1981–1982 fur season, but trapped two or three per year in previous years in the Pass Creek area; he also purchased seven or eight local raccoon in the past five years.

Ronald Yates, a statewide fur buyer from Casper, Natrona Co., purchased 300 raccoon pelts in the 1981–1982 season and approximately 1500 locally during the past five years. He also purchased about 50 in 1981–1982, 300 to 400 in the past five years, out of the Green River drainage system. He stated that raccoons are now being taken where none have been found previously. Mr. Yates stated unequivocally that raccoon are currently present in all of the major drainage systems in the state of Wyoming, bar none. Raccoon from the Snake River drainage are of especially high quality, and there seems to be an abundance of animals along the Big Horn River in the general vicinity of Thermopolis, Hot Springs Co. He also suggested that the Shoshone River may well have served as a dispersal corridor into Wyoming from the Big Horn River, Montana, where, as a boy, he was aware of abundant raccoon populations.

In summary, there is strong evidence that significant populations of raccoon presently occur in areas of suitable habitat throughout the state of Wyoming.

Literature Cited

Clark, T. W., V. A. Saab, and D. Casey. 1980. A partial bibliography of Wyoming mammals. Northwest Sci. 54(1):55–67.

Hall, E. R. 1981. Mammals of North America. John Wiley and Sons, N.Y. 1181 pp.

Hoffmann, R. S., P. L. Wright, and F. E. Newby. 1969. The distribution of some mammals in Montana. J. Mammal. 50(3):579–604.

Long, C. A. 1965. The mammals of Wyoming. Univ. Kansas. Publ., Mus. of Nat. Hist. 14(18):493–758.

Lotze, J. H., and S. Anderson. 1979. *Procyon lotor.* Mamm. Species 119:1–8.

INTERCANINE CROWN DISTANCES IN RED FOXES AND BADGERS

E. Blake Hart[1]

Abstract.— Intercanine crown distances of 605 wild South Dakota red foxes and 249 badgers of unknown age were measured; adults and juveniles were diagnosed by radiographs of canine teeth. In foxes, T-tests between similar age, between similar sex, and between combined age groups were significant at .01. In badgers, significance was found only between adult males and juvenile males and between adult males and adult females at .05.

With refinement of furbearer management practices, methodology of accurate age determination is paramount in obtaining information on current population status. Various workers (Churcher 1960, Grue and Jensen 1976, MacPherson 1969, Morris 1972) have shown that a variety of cranial characters are correlative with the aging process in carnivores.

In the red fox, for example, several skull characters have been shown by some of the above to be reliable indicators of age, such as closure of various sutures, triangularity of postorbital processes, texture of temporal areas, pointedness of nasals, and several dental characters that include numbers of incremental annuli, pulp cavity size, enamel line distance, overall tooth wear, etc. Churcher (1960) was able to differentiate with a fair degree of accuracy between sexes of similarly aged fox by graphing mastoid width against total skull length × zygomatic width.

An additional character that was thought to possibly have correlation with aging in wild populations of red foxes and badgers is the distance between crowns of normally rooted canine teeth.

Upper jaws of over 600 unknown age red foxes and lower jaws of 249 unknown age badgers were obtained from a local fur dealer and were cut from skulls with pruning shears. Measurements of maxillary intercanine crown distances were then made with vernier calipers to the nearest 0.1 mm. Jaws were boiled to loosen canines, after which teeth were removed and X-rayed to distinguish between juveniles and adults. Results were then analyzed to determine significance (Figure 1).

In foxes, all T-tests computed between similar age, similar sex groups, and combined age groups were significant at 0.1; a T-test between adult females and juvenile males was not significant at .05.

In badgers, T-tests between adult and juvenile males and adult males and adult females were significant at .05. No significance (.05) was encountered between adult females and juvenile females, between juvenile males and juvenile females, and between combined adults and combined juveniles.

This study was based upon unknown age South Dakota carnivores that were partitioned as either adults or juveniles by relative size (X-ray) of pulp cavity, an accepted technique among many wildlife workers. These results should be interpreted with the knowledge that relative pulp cavity size has yet to be shown as absolute.

It is hoped that these results will stimulate further studies of intercanine crown distances in known age wild foxes and badgers.

Literature Cited

Churcher, C. S. 1960. Cranial variation in the North American red fox. J. Mammal. 41(3):349–360.

Grue, H., and B. Jensen. 1976. Annual cementum structures in canine teeth in arctic foxes (*Alopex lagopsusil*). Danish Rev. of Game Biol. 10(3):1–12.

Morris, P. 1972. A review of mammalian age determination. Mamm. Rev., 2:69–104.

MacPherson, A. H. 1969. The dynamics of Canadian arctic fox populations. Canadian Wildl. Serv. Rept., Series 8. 52 pp.

---

[1] Department of Mathematics and Natural Sciences, Northern State College, Aberdeen, South Dakota 57401.

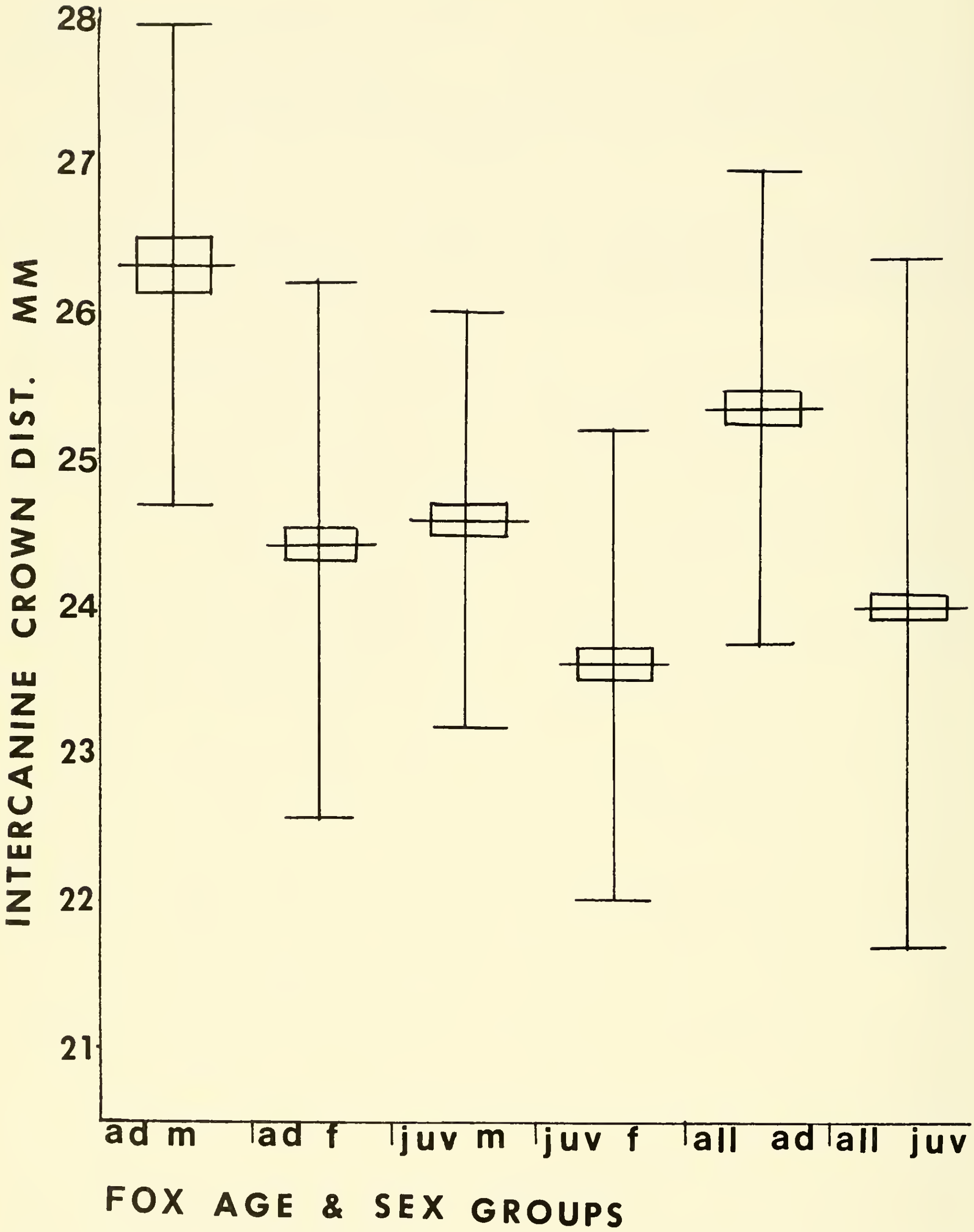


Fig. 1. Maxillary intercanine crown distances of wild South Dakota red foxes. Adults were partitioned from juveniles by X-rays of canine teeth. Means, longer horizontal lines; two standard errors, boxes; and two standard deviations, vertical lines.

INDEX TO VOLUME 42

The genera and species described as new to science in this volume appear in bold type in this index.

A description of Timpie Springs, Utah, with a preliminary survey of the aquatic macrobiota, p. 77.
A new species of *Cryptantha* (Boraginaceae) from Nevada, p. 196.
A new species of *Penstemon* (Scrophulariaceae) from the Uinta Basin of Utah and Colorado, p. 367.
A species of *Cryptantha* (Boraginaceae) dedicated to the memory of F. Creutzfeldt, p. 203.
Additions to the vascular flora of Montana and Wyoming, p. 413.
Algal populations in Bottle Hollow Reservoir, Duchesne County, Utah, p. 205.
Allred, Dorald M., article by, p. 415.
Allred, Kelly Wayne, article by, p. 101.
Amphicranus **splendens**, p. 223.
Andersen, Ferron L., Lauritz A. Jensen, and Jordan C. Pederson, article by, p. 351.
Andersen, Ferron L., Lauritz A. Jensen, and Peter M. Schantz, article by, p. 65.
Ants of Utah, p. 415.
Araptus **micropilosus**, p. 224.
Araptus **morigerus**, p. 224.
Araptus **placetulus**, p. 225.
Austin, D. D., and Philip J. Urness, article by, p. 512.
Austin, George T., and J. Scott Miller, article by, p. 232.
Avery, David F., and Wilmer W. Tanner, article by, p. 273.
Baugh, Thomas M., Michael A. Nelson, and Floyd Simpson, article by, p. 77.
Behavior and habitat preferences of ring-necked pheasants during late winter in central Utah, p. 562.
Bowers, Janice E., article by, p. 105.
Bowers, Michael A., article by, p. 589.
Briggs, George M., and James A. MacMahon, article by, p. 50.
Brotherson, Jack D., article by, p. 246.
Brotherson, Jack D., and Jeffrey G. Skousen, article by, p. 562.
Brotherson, Jack D., and Miles O. Moretti, article by, p. 81.
Brotherson, Jack D., Joy D. Cedarleaf, and S. Dick Worthen, article by, p. 91.
Buccal floor of reptiles, a summary, p. 273.
Campbell, Thomas M., III, Tim W. Clark, and Craig R. Groves, article by, p. 100.
Campbell, Thomas M., III, Tim W. Clark, David G. Socha, and Denise E. Casey, article by, p. 572.
Campos, E. G., and R. B. Eads, article by, p. 241.
Carter-Lovejoy, Steven H., article by, p. 113.
Casey, Denise E., Tim W. Clark, Thomas M. Campbell III, and David G. Socha, article by, p. 572.
Cedarleaf, Joy D., S. Dick Worthen, and Jack D. Brotherson, article by, p. 91.
Chatterley, L. Matthew, Blaine T. Welsh, and Stanley L. Welsh, article by, p. 385.
Chramesus **bispinus**, p. 225.
Cirsium eatonii var. **harrisonii**, p. 200.
Cirsium eatonii var. **murdockii**, p. 200.
Cirsium **ownbeyi**, p. 200.
Cirsium scariosum var. **thorneae**, p. 201.
Cirsium **virginensis**, p. 201.
Clark, Tim W., Thomas M. Campbell III, and Craig R. Groves, article by, p. 100.
Clark, Tim W., Thomas M. Campbell III, David G. Socha, and Denise E. Casey, article by, p. 572.
Cnesinus **aquihuai**, p. 226.
Cnesinus **meris**, p. 226.
Cooper, James J., article by, p. 60.
Courtenay, Walter R., Jr., and James E. Deacon, article by, p. 361.
Crataegus douglasii var. **duchesnensis**, p. 10.
Creasy, James, and Robert B. Finley, Jr., article by, p. 360.
Cryptantha **creutzfeldtii**, p. 203.

Cryptantha **welshii**, p. 196.
Deacon, James E., and Paul Gregor, article by, p. 549.
Deacon, James E., and Walter R. Courtenay, Jr., article by, p. 361.
Dendrocranulus **gracilis**, p. 227.
Description of a new *Phalacropsylla* and notes on *P. allos* (Siphonaptera: Hystrichopsyllidae), p. 241.
Description of the female of *Phalacropsylla hamata* (Siphonaptera: Hystrichopsyllidae, p. 96.
Diameter-weight relationships for juniper from wet and dry sites, p. 73.
Distribution and relative abundance of fish in Ruth Reservoir, California, in relation to environmental variables, p. 529.
Distribution of the moss family Grimmiaceae in Nevada, p. 583.
Dorn, Robert D., and Robert W. Lichvar, article by, p. 413.
Dorsal hair length and coat color in Abert's squirrel (*Sciurus aberti*), p. 597.
Eads, R. B., and E. G. Campos, article by, p. 241.
Eads, R. B., and G. O. Maupin, article by, p. 96.
Early development of the razorback sucker, *Xyrauchen texanus* (Abbott), p. 553.
Ecomorphology and habitat utilization of *Echinocereus engelmannii* and *E. triglochidiatus* (Cactaceae) in southeastern California, p. 353.
Effects of defoliation on reproduction of a toxic range plant, *Zigadenus paniculatus*, p. 524.
Emmerson, Frederick H., article by, p. 350.
England, John Larry, article by, p. 367.
Finley, Robert B., Jr., and James Creasy, article by, p. 360.
First record of pygmy rabbits (*Brachylagus idahoensis*) in Wyoming, p. 100.
First specimen of the spotted bat (*Euderma maculatum*) from Colorado, p. 360.
Flinders, Jerran T., William D. Steigers, Jr., and Susan M. White, article by, p. 567.
Greger, Paul, and James E. Deacon, article by, p. 549.
Groves, Craig R., Thomas M. Campbell III, and Tim W. Clark, article by, p. 100.
Growth of juvenile American lobsters in semiopen and closed culture systems using formulated diets, p. 67.
Gustafson, Eric S., and W. L. Minckley, article by, p. 553.
Habitat manipulation for reestablishment of Utah prairie dogs in Capitol Reef National Park, p. 517.
Hancock, Denis C., Jr., and Donald J. Nash, article by, p. 597.
Hansen, Richard M., and James G. MacCracken, article by, p. 45.
Hart, E. Blake, articles by, p. 599, 601.
Hassler, Thomas J., and Steven Vigg, article by, p. 529.
Heckmann, R. A., S. R. Wadley, R. C. Infanger, and R. W. Mickelsen, article by, p. 67.
Herpetological notes from the Nevada Test Site, p. 219.
Higgins, Larry C., and Kaye H. Thorne, article by, p. 196.
Hylastes **retifer**, p. 227.
Hylocurus **prolatus**, p. 228.
Infanger, R. C., S. R. Wadley, R. A. Heckmann, and R. W. Mickelsen, article by, p. 67.
Insular biogeography of mammals in the Great Salt Lake, p. 589.
Intercanine crown distances in red foxes and badgers, p. 601.
Invertebrate faunas and zoogeographic significance of lava tube caves of Arizona and New Mexico, p. 405.
Jensen, Lauritz A., Ferron L. Andersen, and Peter M. Schantz, article by, p. 65.
Jensen, Lauritz A., Jordan C. Pederson, and Ferron L. Andersen, article by, p. 351.
Johansen, Jeffrey, Samuel R. Rushforth, and Irena Kaczmarska, article by, p. 205.
Kaczmarska, Irena, Jeffrey Johansen, and Samuel R. Rushforth, article by, p. 205.
Krebill, Richard G., and David L. Nelson, article by, p. 262.
Lavin, Matt, article by, p. 583.
Lichvar, Robert W., and Robert D. Dorn, article by, p. 413.
Local floras of the Southwest, 1920–1980: an annotated bibliography, p. 105.
Lund, R., and T. Weaver, article by, p. 73.
MacCracken, James G., and Richard M. Hansen, article by, p. 45.
MacMahon, James A., and George M. Briggs, article by, p. 50.
Mathiasen, Robert L., article by, p. 120.

Maupin, G. O., and R. B. Eads, article by, p. 96.
Mickelsen, R. W., S. R. Wadley, R. A. Heckmann, and R. C. Infanger, article by, p. 67.
Micracis **burgosi**, p. 228.
Miller, J. Scott, and George T. Austin, article by, p. 232.
Minckley, W. L., and Eric S. Gustafson, article by, p. 553.
Moretti, Miles O., and Jack D. Brotherson, article by, p. 81.
Murphy, Joseph R., and Dwight G. Smith, article by, p. 395.
Nash, Donald J., and Denis C. Hancock, Jr., article by, p. 597.
Nelson, David L., article by, p. 369.
Nelson, David L., and Richard G. Krebill, article by, p. 262.
Nelson, Michael A., Thomas M. Baugh, and Floyd Simpson, article by, p. 77.
Nest site selection in raptor communities of the eastern Great Basin desert, p. 395.
New species of American bark beetles (Coleoptera: Scolytidae), p. 223.
New taxa of thistles (*Cirsium*: Asteraceae) in Utah, p. 199.
Observations on the reproduction and embryology of the Lahontan tui chub, *Gila bicolor*, in Walker Lake, Nevada, p. 60.
Observations on woundfin spawning and growth in an outdoor experimental stream, p. 549.
Occurrence and effect of *Chrysomyxa pirolata* cone rest on *Picea pungens* in Utah, p. 262.
Paspalum distichum L. var. *indutum* Shinners (Poaceae), p. 101.
Peck, Stewart B., article by, p. 405.
Pederson, Jordan C., Lauritz A. Jensen, and Ferron L. Andersen, article by, p. 351.
Penstemon **albifluvis**, p. 367.
Phalacropsis dispar (Coleoptera: Phalacridae), an element in the natural control of native pine stem rust fungi in the western United States, p. 369.
Phloeotribus **perniciosus**, p. 229.
Player, Rodney L., and Philip J. Urness, article by, p. 517.
Prairie dog colony attributes and associated vertebrate species, p. 572.
Preliminary index of authors of Utah plant names, p. 385.
Prevalence of *Elaeophora schneideri* and *Onchocerca cervipedis* in mule deer from central Utah, p. 351.
Pseudothysanoes **fimbriatus**, p. 229.
Pseudothysanoes **pini**, p. 229.
Rhythm of fecal production and protein content for black-tailed jackrabbits, p. 567.
Rushforth, Samuel R., Jeffrey Johansen, and Irena Kaczmarska, article by, p. 205.
Schantz, Peter M., Lauritz A. Jensen, and Ferron L. Andersen, article by, p. 65.
Scolytodes **pilifer**, p. 230.
Scolytus **binodus**, p. 230.
Seasonal foods of coyotes in southeastern Idaho: a multivariate analysis, p. 45.
Simpson, Floyd, Thomas M. Baugh, and Michael A. Nelson, article by, p. 77.
Skousen, Jeffrey G., and Jack D. Brotherson, article by, p. 562.
Smith, Dwight G., and Joseph R. Murphy, article by, p. 395.
Socha, David G., Tim W. Clark, Thomas M. Campbell III, and Denise E. Casey, article by, p. 572.
Species-habitat relationships in an Oregon cold desert lizard community, p. 380.
Status of introduced fishes in certain spring systems in southern Nevada, p. 361.
Steigers, William D., Jr., Jerran T. Flinders, and Susan M. White, article by, p. 567.
Structure of Alpine plant communities near King's Peak, Uinta Mountains, Utah, p. 50.
Tanner, Wilmer W., article by, p. 219.
Tanner, Wilmer W., and David F. Avery, article by, p. 273.
Taxonomic studies of dwarf mistletoes (*Arceuthobium* spp.) parasitizing *Pinus strobiformis*, p. 120.
Temperature and salinity relationships of the Nevadan relict dace, p. 541.
Temperature-related behavior of some migrant birds in the desert, p. 232.
Tepedino, V. J., article by, p. 524.
The raccoon, *Procyon lotor*, in Wyoming, p. 599.
The prevalence of *Echinococcus granulosus* and other taeniid cestodes in sheep dogs of central Utah, p. 65.

The relation between species numbers and island characteristics for habitat islands in a volcanic landscape, p. 113.
Thorne, Kaye H., and Larry C. Higgins, article by, p. 196.
Urness, Philip J., and D. D. Austin, article by, p. 512.
Urness, Philip J., and Rodney L. Player, article by, p. 517.
Utah flora: Rosaceae, p. 1.
Utah plant types—historical perspective 1840 to 1981—annotated list, and bibliography, p. 129.
Vegetal responses and big game values after thinning regenerating lodgepole pine, p. 512.
Vegetation and soil factors in relation to soil position on foothill knolls in the Uinta Basin of Utah, p. 81.
Vegetation of the mima mounds of Kalsow Prairie, Iowa, p. 246.
Vigg, Steven, article by, p. 541.
Vigg, Steven, and Thomas J. Hassler, article by, p. 529.
Wadley, S. R., R. A. Heckmann, R. C. Infanger, and R. W. Mickelsen, article by, p. 67.
Weather conditions in early summer and their effects on September blue grouse (*Dendragapus obscurus*) harvest, p. 91.
Weaver, T., and R. Lund, article by, p. 73.
Welsh, Blaine T., L. Matthew Chatterley, and Stanley L. Welsh, article by, p. 385.
Welsh, Stanley L., articles by, p. 1, 129, 199, 203.
Welsh, Stanley L., L. Matthew Chatterley, and Blaine T. Welsh, article by, p. 385.
Werschkul, David F., article by, p. 380.
Western diamondback rattlesnake in southern Nevada: a correction and comments, p. 350.
White, Susan M., William D. Steigers, Jr., and Jerran T. Flinders, article by, p. 567.
Wood, Stephen L., article by, p. 223.
Worthen, S. Dick, Joy D. Cedarleaf, and Jack D. Brotherson, article by, p. 91.
Yeaton, Richard I., article by, p. 353.

7070 029

NOTICE TO CONTRIBUTORS

Manuscripts intended for publication in the *Great Basin Naturalist* or *Great Basin Naturalist Memoirs* must meet the criteria outlined in paragraph one on the inside front cover. They should be directed to Brigham Young University, Stephen L. Wood, Editor, Great Basin Naturalist, 290 Life Science Museum, Provo, Utah 84602. Three copies of the manuscript are required. They should be typewritten, double spaced throughout on one side of the paper, with margins of at least one inch on all sides. Use a recent issue of either journal as a format, and the *Council of Biology Editors Style Manual, Fourth Edition* (AIBS 1978) in preparing the manuscript. An abstract, about 3 percent as long as the text, but not exceeding 200 words, written in accordance with *Biological Abstracts* guidelines, should precede the introductory paragraph of each article.

All manuscripts receive a critical peer review by specialists in the subject area of the manuscript under consideration. Authors may recommend one or two reviewers for their article.

Accepted manuscripts less than 100 printed pages in length will automatically be assigned to the *Great Basin Naturalist*. Those larger than 100 printed pages will be considered for the *Memoirs* series.

Illustrations and Tables. All illustrations and tables should be made with a view toward having them appear within the limits of the printed page. The original illustrations or glossy photoprints of them should accompany the manuscript. Illustrations should be prepared for reduction by the printer to either single-column (2⅝ inches) or double-column (5½ inches) width, with the length not exceeding 7½ inches.

Costs Borne by Contributor. Contributors to the *Great Basin Naturalist* should be prepared to donate from $10 to $40 per printed page toward publication of their article (in addition to reprint costs). Excessive or complex tables requiring typesetting may be charged to the author at cost. Authors publishing in the *Great Basin Naturalist Memoirs* may be expected to contribute $40 per printed page in addition to the cost of the printed copies they purchase. No reprints are furnished free of charge.

Reprint Schedule for the *Great Basin Naturalist*

100 copies, minimum cost for 2 pages, $26.
Each additional 2 pages, $6.
Each additional 100 copies, $4 for each 2 pages.
Examples: 300 copies of 10 pages = $82; 200 copies of 13 pages = $86.

Great Basin Naturalist Memoirs

No. 1 The birds of Utah. By C. L. Hayward, C. Cottam, A. M. Woodbury, H. H. Frost. $10.
No. 2 Intermountain biogeography: a symposium. By K. T. Harper, J. L. Reveal et al. $15.
No. 3 The endangered species: a symposium. $6.
No. 4 Soil-plant-animal relationships bearing on revegetation and land reclamation in Nevada deserts. $6.
No. 5 Utah Lake monograph. $8.
No. 6 The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. $60.

TABLE OF CONTENTS

Ants of Utah. Donald M. Allred 415

Vegetal responses and big game values after thinning regenerating lodgepole pine. D. D. Austin and Philip J. Urness 512

Habitat manipulation for reestablishment of Utah prairie dogs in Capitol Reef National Park. Rodney L. Player and Philip J. Urness 517

Effects of defoliation on reproduction of a toxic range plant, *Zigadenus paniculatus*. V. J. Tepedino 524

Distribution and relative abundance of fish in Ruth Reservoir, California, in relation to environmental variables. Steven Vigg and Thomas J. Hassler 529

Temperature and salinity relationships of the Nevadan relict dace. Steven Vigg 541

Observations on woundfin spawning and growth in an outdoor experimental stream. Paul Greger and James E. Deacon 549

Early development of the razorback sucker, *Xyrauchen texanus* (Abbott). W. L. Minckley and Eric S. Gustafson 553

Behavior and habitat preferences of ring-necked pheasants during late winter in central Utah. Jeffrey G. Skousen and Jack D. Brotherson 562

Rhythm of fecal production and protein content for black-tailed jackrabbits. William D. Steigers, Jr., Jerran T. Flinders, and Susan M. White 567

Prairie dog colony attributes and associated vertebrate species. Tim W. Clark, Thomas M. Campbell III, David G. Socha, and Denise E. Casey 572

Distribution of the moss family Grimmiaceae in Nevada. Matt Lavin 583

Insular biogeography of mammals in the Great Salt Lake. Michael A. Bowers 589

Dorsal hair length and coat color in Abert's squirrel (*Sciurus aberti*). Denis C. Hancock, Jr., and Donald J. Nash 597

The raccoon, *Procyon lotor*, in Wyoming. E. Blake Hart 599

Intercanine crown distances in red foxes and badgers. E. Blake Hart 601

Index 603

ACME
BOOKBINDING CO., INC.

SEP 9 1983

100 CAMBRIDGE STREET
CHARLESTOWN, MASS.

3 2044 072 231 269